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Cranial Anatomy of the Lower Jurassic Shark *Hybodus reticulatus* (Chondrichthyes: Elasmobranchii), with Comments on Hybodontid Systematics

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ABSTRACT

Hybodus reticulatus Agassiz, from the Lower Jurassic of England, is considered to be the type species of *Hybodus*. It is founded on skeletal fragments and associated teeth. The cranial anatomy is described from several incomplete specimens, including some of the type material. Two specimens from the Upper Lias of Germany are referred to *H. cf. reticulatus*. Comparisons are made with the Lower Cretaceous *Hybodus basanus*, whose cranial morphology is more completely known. The neurocranium and jaws are similar in these species, suggesting that many of the anatomical peculiarities noted in the ethmoid and otico-occipital regions of *H. basanus* characterize a larger group of hybodontid sharks, including the type

species of *Hybodus*. Some differences are noted in the detailed arrangement of the lateral otic process, cephalic spines, and ethmopalatine articulation in *H. reticulatus* and *H. basanus*. These differences are considered to be of systematic importance; *H. basanus* and *H. fraasi* are placed in a new genus, *Egertonodus*, on the basis of several differences from *H. reticulatus*. The genus *Hybodus* remains an assemblage of nominal species, but increased anatomical data will gradually alleviate this situation. A list of genera retained within the Hybodontidae is given. Hybodontid tooth histology is reviewed, and forms the basis of a phylogenetic hypothesis which is open to falsification by other anatomical data.

INTRODUCTION

Hybodus is a species-rich genus of Mesozoic elasmobranchs. Most of these nominal taxa are dubious, however, being founded

upon isolated teeth and fin-spines. A few species are known from more complete skeletal material, such as *H. reticulatus*, *H. de-*

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labechei, and *H. hauffianus* from the Lower Jurassic (Agassiz, 1837; Charlesworth, 1839; Day, 1864; Woodward, 1889a, 1889b; Fraas, 1889, 1896; Brown, 1900; Jaekel, 1906; Koken, 1907), *H. fraasi* from the Upper Jurassic (Koken, 1907; Maisey, 1986), and *H. basanus* from the Lower Cretaceous (Egerton, 1845; Woodward, 1889a, 1916, 1919; Maisey, 1982, 1983).

There are a number of problems surrounding the nomenclature and type species of *Hybodus*. The name first appears in Alberti (1834), where *H. plicatilis* is quoted without description from a then-unpublished Agassiz manuscript. The species name is thus unavailable as an indicator for the genus in that work. *Hybodus* was first defined (along with 20 nominal species, including *H. plicatilis*) by Agassiz (1837), but a type species was not designated. Some authors have subsequently regarded *H. plicatilis* as the type species (e.g., Glikman, 1967), but Woodward's (1916, p. 4) designation of *H. reticulatus* takes priority. *Hybodus reticulatus* is consequently retained here as the type species of *Hybodus*.

Of the 20 original *Hybodus* species described by Agassiz (1837), 17 are founded partly or entirely upon teeth or partial dentitions. The remaining three species were based on fin spines; none of these species are considered taxonomically reliable (Woodward, 1889a, p. 250; Maisey, 1978).

Koken (1907, p. 4) commented that *H. reticulatus* was widely regarded as the type species of *Hybodus*, and was extremely critical of Jaekel's (1889) proposal to relegate *Hybodus* to a form genus of fin spine, particularly since Jaekel's (op. cit.) new genus *Orthybodus* supposedly included *Hybodus reticulatus* (see comments on taxonomy in the latter part of this work). Thus the grounds for regarding *H. reticulatus* as the type species of *Hybodus* are well established.

From a pragmatic viewpoint, Woodward's (1916) proposal is highly justified: (1) the species has page priority over others founded upon teeth; (2) it is one of the three original species known both from teeth and fin spines; (3) it is represented by skeletal material (including some of the original specimens), unlike the majority of other *Hybodus* spp.; and (4) it is the first *Hybodus* species to be reliably figured (*in de la Beche*, 1822).

Hybodus reticulatus is one of several species occurring in the Lower Lias of Lyme Regis in Dorset, England. There are also some early references to *H. reticulatus* from the Upper Lias of Germany; fin spines and a fragment of mandible with teeth from Ohmden were described by Quenstedt (1858, p. 222, pl. 27, fig. 1; 1885, p. 274, pl. 21, fig. 1). Woodward (1889a, p. 268) also noted "an undetermined species allied to *Hybodus reticulatus*" from the Upper Lias of Boll, Württemberg, represented by BM(NH) P5880. According to Fraas (1896), all these German specimens are referable to another species, *H. hauffianus*. The latter has since become known from magnificent complete specimens (Brown, 1900; Koken, 1907; Hauff and Hauff, 1981), and is widely envisioned as a "typical" shark of the Mesozoic (e.g., Romer, 1945; Gregory, 1951; Schaeffer, 1967). Fraas (1896) distinguished *H. hauffianus* from *H. reticulatus* on stratigraphic grounds and on differences in the teeth and fin spines.

A recently acquired specimen at the Staatliches Museum für Naturkunde (Stuttgart; catalog no. 52460) has more gracile and acuminate teeth than *H. hauffianus* from the same stratigraphic horizons (see latter part of this paper). The teeth of this specimen are reminiscent of *H. reticulatus* in having vertical lingual and labial striations confined to the lower two-thirds of the crown (cf. *H. hauffianus* teeth which are more extensively striated and have relatively shorter cusps; Fraas, 1896). Other Hybodontidae with similar teeth to *H. reticulatus* include *H. plicatilis* (Muschelkalk of Germany and France) and *H. basanus* (Wealden of Southern England).

Fortuitously, *H. reticulatus* is represented by a number of incomplete skeletons and skeletal fragments associated with teeth, all from Lyme Regis (the type locality). Only material having teeth identical with Agassiz's original specimens has been included in the present hypodigm.

ACKNOWLEDGMENTS

I thank Drs. Patterson and Forey for permitting preparation and study of *H. reticulatus* specimens in the British Museum (Natural History), and for allowing me to borrow material for closer examination. My thanks

are also extended to Dr. Powell (Oxford), Dr. M. D. Crane (Bristol City Museum and Art Gallery), and Ms. Alison Longbottom (British Museum) for their efforts in tracking down actual and purported Agassiz type specimens. Dr. R. Wild kindly allowed me to study the Holzmaden sharks in the Stuttgart collection including the new specimen resembling *H. reticulatus*, and Dr. P. Wellnhofer generously allowed me access to the holotype of *H. fraasi* in Munich. Preparation of BM(NH) and Stuttgart specimens was undertaken at the American Museum by Walter Sorensen and Ed Pederson. Illustrations were prepared by Ellen Garvens, Peter Goldberg, and Frank Ippolito. The manuscript was typed by Alejandra Lora and edited by Brenda Jones. This work is an integral part of a project concerning Mesozoic Hybodontidae, and is funded by the National Science Foundation (Award no. BSR 8308419). I thank Drs. G. Johnson (University of South Dakota) and B. Schaeffer (AMNH) for critically reviewing the MS, and Drs. L. Herman and P. Meylan (AMNH) for discussing the nomenclatural situation.

ABBREVIATIONS

Institutional

AMNH	American Museum of Natural History
BCM	Bristol City Museum, England
BM(NH)	British Museum (Natural History)
MCZ	Museum of Comparative Zoology, Harvard
OUM	Oxford University Museum, England
SMNS	Staatliches Museum für Naturkunde in Stuttgart

Anatomical

acl	accessory lateral cusp
acm	accessory mesial cusp
add f	adductor fossa
afsp	anterior fin spine
art cot	articular cotylus
art k	articular knob
art pr	articular process
ba	barb
bh	basihyal
bp	basal plate
c	crown
cbr	ceratobranchial
ch	ceratohyal
cik	caudal internasal keel
crd	dorsal crest
crl	lateral crest

crm	mesial crest
crp	posterior crest
csp	cephalic spine
ebr	epibranchial
ect pr	ectethmoid process
end f	endolymphatic fossa
ethp pr	ethmopalatine process
feha	foramen for efferent hyoidean artery
fica	foramen for internal carotid artery
fm	foramen magnum
fora	foramen for orbital artery
glda	groove for lateral dorsal aorta
hbr	hypobranchial
hym VII	hyomandibular branch of facial nerve
hyp l	hypotic lamina
hy r	hyoid rays
jc	jugular canal
lab	labial cartilage
ll	lateral lobe
lm	mesial lobe
lot pr	lateral otic process
lp	posterior lobe
Mc	Meckel's cartilage
mil	lateral marginal indentation
mim	mesial marginal indentation
not c	notochordal canal
not f	notochordal foramen
oc ar	occipital arch
oc cot	occipital cotylus
olfc	olfactory canal
ot cap	otic capsule
pbr	pharyngobranchial
po pr	postorbital process
pq	palatoquadrate
pr cf	precerebral fontanelle
prf com	prefacial commissure
q con	quadrate concavity
q fl	quadrate flange
rb	rostral bar
sc	scapulocoracoid
sof	spino-occipital foramen
sp c	spinal canal
sub s	suborbital shelf
sup cr	supraorbital crest
t	teeth
vgf	vagus-glossopharyngeal fossa
II	optic nerve
V	trigeminal nerve
VII	facial nerve
IX	glossopharyngeal nerve
X	vagus nerve

Orientation (teeth)

lab	labial
lat	lateral
ling	lingual
occl	occlusal

CLASS CHONDRICHTHYES

SUBCLASS ELASMOBRANCHII

PLESION HYBODONTIFORMES

FAMILY HYBODONTIDAE OWEN, 1846

EMENDED DIAGNOSIS: Elasmobranchs with two dorsal fin spines having alternated posterior denticles near the midline, and smooth unenameled ribbing which may be continuous proximally or broken up into rows of wrinkled and radially striated tubercles; fin-spine trunk osteodentine has distinct concentric layering; paired cephalic spines (one or two pairs) present in males; teeth with anaulacorhize basal platform and tumid to multicuspid crown.

SYSTEMATIC NOTE: The term "Plesion" here follows the use outlined by Patterson and Rosen (1977). Hybodontiformes may be further sequenced into nested taxa, using a suite of anatomical characters, but to do so at this point would be premature since several taxa are awaiting revision (Maisey, in prep.). Some of the anatomical differences noted below between species of *Hybodus* are slight, even trivial, and one could argue *ad nauseam* over the relative merits of "lumping" and "splitting." Modern elasmobranch teeth are usually distinctive at generic level, but there are cases of similar teeth occurring in apparently different genera (e.g., various carcharhinids, particularly those with "*Physodon*" teeth; Applegate, 1978; Compagno, 1979; Cappetta, 1980). Rarer cases of different tooth morphology supposedly within one genus (e.g., "*Mustelus*") are perhaps an artifact of systematic inattention.

From this point on within the present paper, taxa with teeth similar to those of *Hybodus reticulatus*, but whose anatomy otherwise differs only slightly or else is unknown, continue to be referred to *Hybodus*. Following a discussion of the cranial morphology of *H. reticulatus*, two *Hybodus* species (*H. basanus*, *H. fraasi*) are removed to a new genus; until then they are also referred to *Hybodus* in the text. Eventually it is hoped that a broader systematic scheme will be generated in which other species will be either placed more firmly within *Hybodus* or else removed to other genera. For those unfortunates working primarily with isolated teeth, it is rec-

ommended that, as in the present work, these indeterminate remains be referred to *Hybodus* until some generically diagnostic characters (either from more complete material or from the teeth themselves) are identified.

Genus *Hybodus* Agassiz

DIAGNOSIS: Hybodontidae with an ethmopalatine articulation extending into the midorbital region and with a subocular fold in the posterior part of the orbit to accommodate the dorsal margin of palatoquadrate; basicranium with deep aortic grooves exposed for their entire length; multicuspid acuminate teeth with osteodont crowns.

TYPE SPECIES: *Hybodus reticulatus* Agassiz.

Hybodus reticulatus Agassiz

1822, "Fossil jaw with a triple row of teeth," H. T. de la Beche, p. 44, pl. 5, fig. 3.

1837-43, *Hybodus reticulatus* Agassiz, vol. 3, pp. 50, 180, pl. 9, figs. 1-9 (some may pertain to *Acrodus*); pl. 24, fig. 26; pl. 22a, figs. 22, 23.

1889a, *Hybodus reticulatus*: Woodward, p. 266, pl. 10, figs. 16-18.

1907, *Hybodus reticulatus*: Koken, p. 3.

1916, *Hybodus reticulatus*: Woodward, p. 4 (designated type species).

1966, *Hybodus reticulatus*: Patterson, p. 287.

LECTOTYPE: Bristol City Museum C4727, right mandible with teeth and labial cartilages; see figures 1, 2; also Agassiz (1837, pl. 24, fig. 26).

LOCALITY AND HORIZON: Lyme Regis, Dorset, England. Lower Lias (Sinemurian Stage), Lower Jurassic.

DIAGNOSIS: Teeth narrow, with a relatively high crown, the median eminence and all the lateral cones slender and sharply pointed; superficial coronal wrinkles fine and numerous, often not extending to the apex; the principal cusp of anterior and anterolateral teeth between two-thirds and three-quarters the breadth of the tooth, usually recurved both posteriorly and lingually; supraotic cephalic spines with low accessory cusps.

REFERRED MATERIAL:

J3088, Oxford University Museum, scattered teeth and cartilage fragments (Philpot coll.).

J3920, broken mandible with teeth, Philpot coll.

J3099, fin spine, Philpot coll.

J3100, fin spine, Philpot coll.

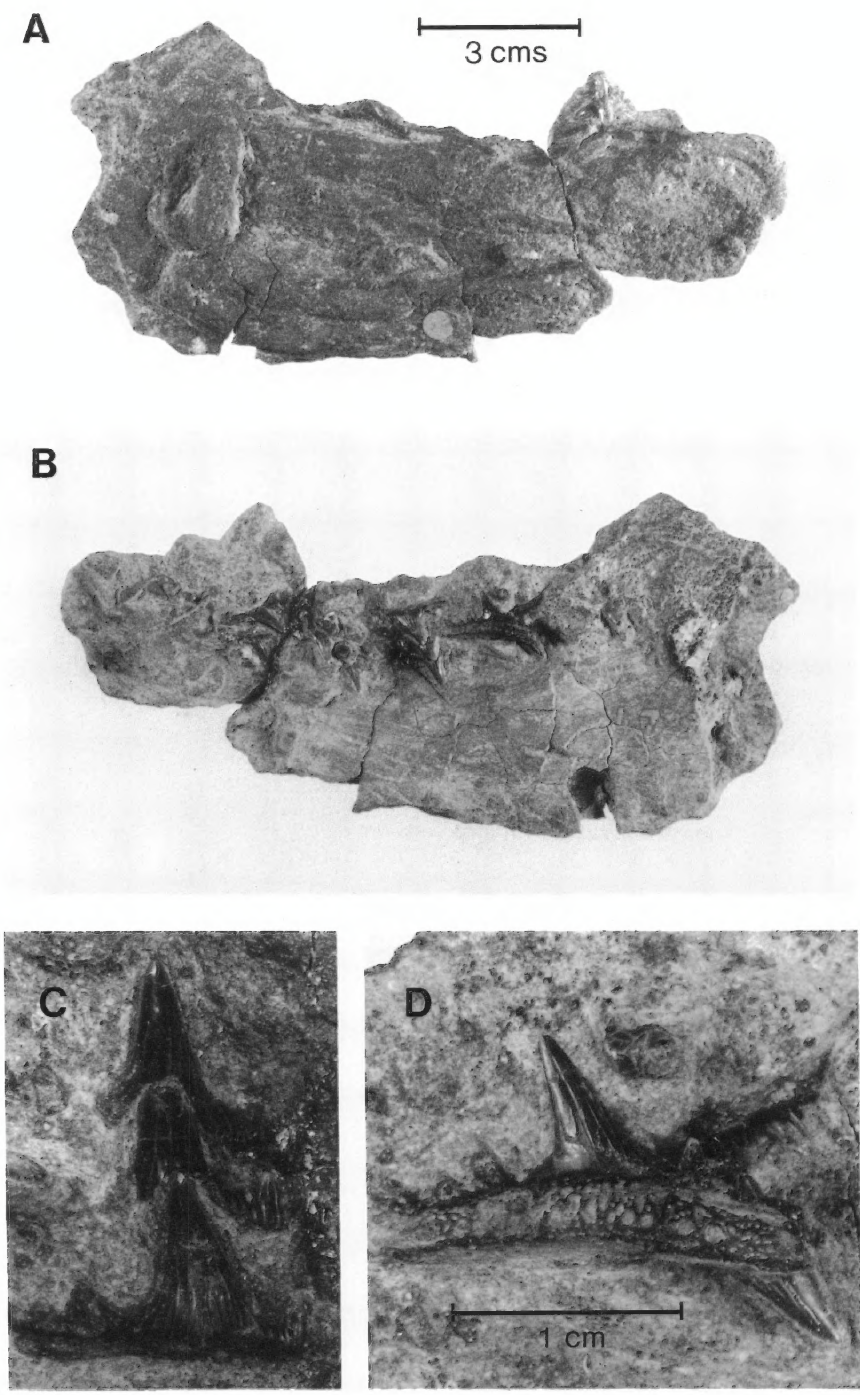


Fig. 1. *Hybodus reticulatus*, BCM C4727, lectotype, figured Agassiz, 1837, pl. 24, fig. 26; right mandible with associated teeth (shown enlarged in C and D) and labial cartilages; **A**, lateral view; **B**, mesial view. C and D enlarged to same scale.

J3109, fin spine, Philpot coll.
J3318, fin spine.

C4725, Bristol City Museum, fin spine; syntype,
figured Agassiz (1837, pl. 9, fig. 5).

- BM(NH) 40335, crushed head with teeth and shagreen (some teeth figured Woodward, 1889a, pl. 10, figs. 16–18), purchased from J. Tennant, 1867.
- BM(NH) P3160, crushed head with scattered dentition and both fin spines (Enniskillen coll.).
- BM(NH) P3162, scattered teeth and cartilage fragments (Enniskillen coll.).
- BM(NH) P3163, crushed head with palatoquadrate and teeth (Enniskillen coll.).
- BM(NH) P2198, fragment of cartilage with shagreen and teeth (Egerton coll.).
- BM(NH) P2198a, parts of mandibular arch with teeth and cephalic spine (Egerton coll.).
- BM(NH) P2198b, two groups of teeth (Egerton coll.).
- BM(NH) P2203a, broken teeth and cephalic spines (Egerton coll.).
- BM(NH) P2203b, broken teeth and cephalic spines (Egerton coll.).
- BM(NH) P2203d, occiput, part of left palatoquadrate, tooth and two cephalic spines (Egerton coll.).
- BM(NH) P2208, crushed head with teeth, three incomplete cephalic spines and fin spine.
- BM(NH) P3168, crushed head and anterior trunk region of juvenile (Enniskillen coll.).
- BM(NH) P3156, crushed head with traces of teeth, two cephalic spines and a fin spine (Enniskillen coll.).
- BM(NH) P5876, fragmentary head with teeth and fin spines (Enniskillen coll.).
- BM(NH) P4355, fin spine, apparently a syntype figured Agassiz (1837, pl. 9, fig. 2).
- MCZ 780, fragments of large jaws with a few teeth.
- MCZ 816, crushed head with part of palatoquadrate, shagreen and teeth (Marder coll.).

NOTES ON THE MATERIAL

The first illustration of a jaw fragment with *Hybodus* teeth was published by de la Beche (1822, p. 44, pl. 5, fig. 3). The figure of this specimen, by then identified by Agassiz (1837) as *Hybodus reticulatus*, was reproduced in the "Bridgewater Treatises" (Buckland, 1837, pl. 27d, figs. C1 and 2). According to Woodward (1889a, p. 266) the original specimen ("Associated teeth, cartilage, and dorsal spines") is in the "Oxford Museum" (i.e., Oxford University Museum).

The earliest reliable account of this and other specimens was published by Agassiz (1837). However he did not designate any particular specimen as a holotype. His original material has become scattered and much

is now lost. Furthermore, some institutions hold specimens that have been regarded as forming part of Agassiz's type series but which bear little or no resemblance to his figured examples. Among these are J3088 (Oxford University Museum, Philpot coll.) and BM(NH) P2166. J3088 bears an Agassiz label, numbered 43c X; it had been identified as a doubtful syntype, thought to be the specimen figured by Agassiz (1837, pl. 24, fig. 26). In fact, the specimen figured there is in the Bristol City Museum (C4727). J3088 cannot be recognized as one of the specimens figured by Agassiz (1837), nor as the one shown by de la Beche (1822) or Buckland (1837). It is in a fragmentary state, however, and could conceivably have once been the original piece. BM(NH) P2166 is one fin spine of many originally cataloged under that number (now assigned other numbers). It had been considered one of the spines figured by Agassiz (1837, pl. 9, fig. 5), but this spine is also in Bristol (C4725). There is no evidence that the two Bristol specimens, nor the fin spine BM(NH) P4355, pertain to the same individual. The other original specimens are now considered lost. In view of the nondiagnostic nature of the fin spines C4725 and P4355, the mandible and associated teeth, C4727 is here designated the lectotype of *Hybodus reticulatus*.

In Agassiz (1837, pl. 24), this specimen is figured in inner as well as outer aspects. Curiously, the inner view was incompletely figured and seems smaller than the outer view because the posterior part of Meckel's cartilage, with its mandibular joint, is not shown (this can be seen in the photograph of the complete specimen, fig. 1).

According to Woodward (1889a, p. 266), a fin spine referred to *H. formosus* by Agassiz (1837, pl. 9, figs. 11, 12) pertains to *H. reticulatus*, although Woodward (op. cit., p. 267) went on to admit that, "dorsal fin-spines of this species are not readily distinguishable from those of *Acrodus anningiae*," which he regarded as a valid taxon, and he gave no reason for reassigning Agassiz's specimen.

The following specimens, referred to *H. reticulatus*, have been prepared using acetic acid and mechanical techniques: BM(NH) P2208, P2203d, MCZ 780, and MCZ 816.

Of the material listed earlier, BM(NH) P3168 was identified as *H. raricostatus* by Woodward (1889a, p. 258), and another (P3160) was identified as *H. delabechei* (ibid., p. 260). I consider the tooth morphology of these specimens to be more like that of *H. reticulatus*, however. P3168 is a small individual, and any slight differences in its teeth may be accounted for as ontogenetic variation like that noted in *H. basanus* (Maisey, 1983, p. 52). Since other specimens of *H. delabechei* and *H. raricostatus* equal those of *H. reticulatus* in size, these species are still considered distinct on the basis of tooth morphology.

One of the most informative specimens of *Hybodus reticulatus* is BM(NH) P2208 (figs. 2, 3). A complete but damaged braincase is preserved, with three cephalic spines in situ on the dorsal surface of the otico-occipital region. A large part of the cranium is visible dorsally. In addition the inner wall of the left orbit is displaced laterally so that some features are discernible within it. The braincase of P2208 is not well preserved, however, and it would be almost impossible to interpret much of the finer morphology without reference to *H. basanus* (see Maisey, 1982, 1983). All but the most anterior extremity of the left palatoquadrate is well preserved. The posterior half of the left mandible (Meckel's cartilage) is also present. The jaws of the left side are preserved in their original articular relationship, along with the ceratohyal and hyomandibula. Behind the head are some pieces of the branchial skeleton, parts of which appear to be undisturbed. The coracoid moiety of one scapulocoracoid is also present below the branchial skeleton.

Part of the basicranium is exposed in BM(NH) P3168, a small and presumably juvenile specimen seen in ventral aspect. The right mandible is missing, but the right palatoquadrate is exposed in ventral/mesial view, and its mandibular joint is visible (fig. 4). The ceratohyals and basihyal lie centrally over the braincase. Parts of the occiput and branchial arches are also discernible. The ethmopalatine region is damaged and incomplete.

A complete and uncrushed occipital cotylus is preserved in BM(NH) P2203D (fig. 5). This fragment (associated with a tooth and

two cephalic spines) shows the posterior ends of the aortic grooves on its ventral (external) surface, and part of the calcified notochordal canal internally.

MCZ 780 comprises a great many fragments of a large head. The best preserved parts are from the jaws of the left side. A substantial part of the left palatoquadrate is intact, as is the posterior part of the corresponding mandible.

BM(NH) P3160 displays the neurocranium in ventral view, although part of the left side is obscured by other pieces of cartilage (fig. 6). This specimen has provided most of the information on the basicranium presented below.

From the material available it seems that the cranial anatomy of *H. reticulatus* is very similar to that of *H. basanus* (fig. 7; cf. Maisey, 1982, 1983). Preservation of *H. reticulatus* does not approach that of *H. basanus* in quality, however, and consequently a number of aspects remain doubtful or unknown in the type species.

DESCRIPTION

THE NEUROCRANIUM

Since almost all the specimens of *H. reticulatus* are crushed, the general proportions of the braincase can only be estimated. The intact occiput in BM(NH) P2203D (fig. 5) is proportioned as in *H. basanus* (e.g., BM(NH) P60110; Maisey, 1983, figs. 4, 5) and the overall shape and proportions of the braincase in dorsal and ventral views (figs. 2, 3, 6) are also close to those of *H. basanus*. Therefore the neurocranium of *H. reticulatus* and *H. basanus* are thought to have been similarly proportioned. The braincase is widest between the postorbital processes. The orbits lie approximately midway along the braincase, and are underlain by a suborbital shelf (figs. 6, 7). The postorbital process has a slight anterior inclination distally, giving the orbit an oval outline (P2208; MCZ 816). Nasal capsules are not preserved, although part of the olfactory canal is present in P2208, lateral to the precerebral fontanelle (fig. 3). The ethmoid region is prismatically calcified, even in the presumed juvenile specimen P3168 (fig. 4). This suggests early calcification of the eth-



Fig. 2. *Hybodus reticulatus*, BM(NH) P2208, complete but damaged head in dorsolateral view.

moid region, as in *H. basanus* and Permian xenacanth (Schaeffer, 1981; Maisey, 1983). The ethmoid region constitutes about a quarter of the braincase length, as in *H. basanus* and *Tristychius* (Dick, 1978). This is more than in certain Paleozoic sharks (e.g., *Cobelodus*, *Tamiobatis*, *Xenacanthus*; Romer, 1964; Zangerl and Case, 1976; Schaeffer, 1981), but less than in most living sharks.

The olfactory canal is large in P2208, and has a mesial wall (cf. *H. basanus*). There is an additional canal within the lateral wall of the internasal lamina, mesial to the olfactory canal. A corresponding canal in "*H.*" *basanus* was interpreted as possibly housing an anteromedially directed branch of the lateral ophthalmic nerve (Maisey, 1983, p. 13). The floor of the precerebral fontanelle contains a foramen leading into a canal (P2208), as in *H. basanus*. I have previously suggested that this canal housed the anterior cerebral vein, and that it lay close to the floor of the olfactory canal (Maisey, 1983, p. 17). There is nothing inconsistent with this view in *H. re-*

ticulatus, although the olfactory canal seems better calcified than in *H. basanus*.

The ventral surface of the internasal septum is folded into a median keel in P3160 (fig. 6), and traces of this keel are also visible along the broken anterior edge of P2208. The floor of the precerebral fontanelle is fairly flat and does not contribute to the keel. The arrangement therefore closely resembles that in *H. basanus*, although in *H. reticulatus* the keel is a little wider relative to the rest of the ethmoid region (fig. 7). Comparison with *H. basanus* suggests that this keel did not form part of any rostral structure. A comparable keel is also found in *Xenacanthus* and *Tamiobatis* (Schaeffer, 1981).

In *H. basanus* a bulbous ethmopalatine process arises from each side of the internasal keel, ventral to the precerebral fontanelle and olfactory canals (Maisey, 1983, figs. 2, 3, 8, 9, 12, 13, 14, 16). This process provides an important articulation with the palatoquadrate, whose dorsal margin lies within a rounded groove between the ethmopalatine process

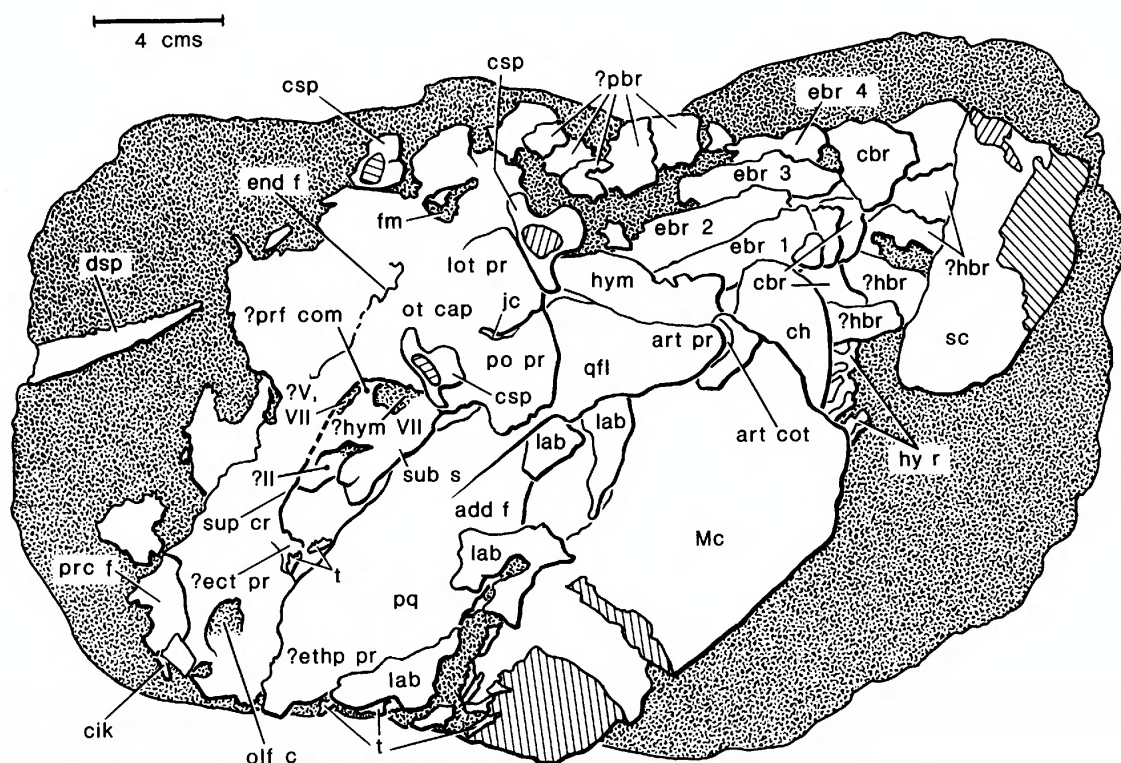


Fig. 3. Annotated key to principal features displayed by BM(NH) 2208.

and palatobasal ridge. In *H. basanus* the palatoquadrate has a short dorsal flattened area which articulates with the ventral surface of the ethmopalatine process.

This articular surface is also present in *H. reticulatus*, but evidence for the cranial ethmopalatine process is poor. In P2208, however, the badly crushed left ethmopalatine process seems to be present, immediately overlying a corresponding flattened articular surface of the palatoquadrate. In P3160 parts of what may be the left ethmopalatine process are exposed lateral to the internasal keel. In this specimen that is also evidence for a short median rostral bar. Its shape suggests that *H. reticulatus* had a somewhat longer median rostral bar than in *H. basanus* and *H. fraasi*.

The suborbital shelf of P3160 tapers anteriorly until it merges with the internasal keel. In *H. basanus* this shelf is broader below the postnasal wall than farther posteriorly, and then narrows abruptly beneath the ethmopalatine process. Consequently the configuration of the basicranium differs in *H.*

reticulatus and *H. basanus*, although the articular relationship between the braincase and palatoquadrate is essentially similar. In both species the dorsal margin of the palatoquadrate lies within the orbit and overlies the suborbital shelf. In *H. basanus* and *H. fraasi* the suborbital shelf underlies the palatoquadrate only anteriorly (Maisey, 1983, 1986), whereas in *H. reticulatus* this overlap seems to have extended farther toward the postorbital process. The suborbital shelf of P3160 has a distinct groove flanked by oblique ridges toward the rear of the orbit, interpreted as part of an articulation with the palatoquadrate. Topographically this articulation lies much farther posteriorly than in *H. basanus*, and is more comparable with the ethmoidal articulation in "*Cladodus*" and *Xenacanthus* (Gross, 1937; Schaeffer, 1981). In P3160 there is a foramen located immediately posterior to the articulation. Schaeffer (1981) interpreted a similarly positioned foramen in Texas *Xenacanthus* and "*Cladodus*" from Germany as housing the efferent pseudobranchial artery.



Fig. 4. *Hybodus reticulatus*, BM(NH) P3168, jaws and visceral arches in ventral aspect; parts of the occiput and ethmopalatine region are also visible.

The foramen for this vessel in *H. basanus* apparently lies dorsal to the suborbital shelf in the posterior part of the orbit (Maisey, 1983, figs. 9, 13, 14). *Hybodus reticulatus* therefore seems to have its ethmoidal articulation and efferent pseudobranchial foramen arranged as in some Paleozoic sharks and not as in *H. basanus*. I suspect that the

anterior position of the ethmoidal articulation in *H. basanus* and *H. fraasi* is derived relative to the condition in *H. reticulatus*, *Xenacanthus*, and "*Cladodus*."

The only specimen of *H. reticulatus* in which the orbital wall is visible is P2208; even here the cartilage is broken and few features are discernible (figs. 2, 3). Two large

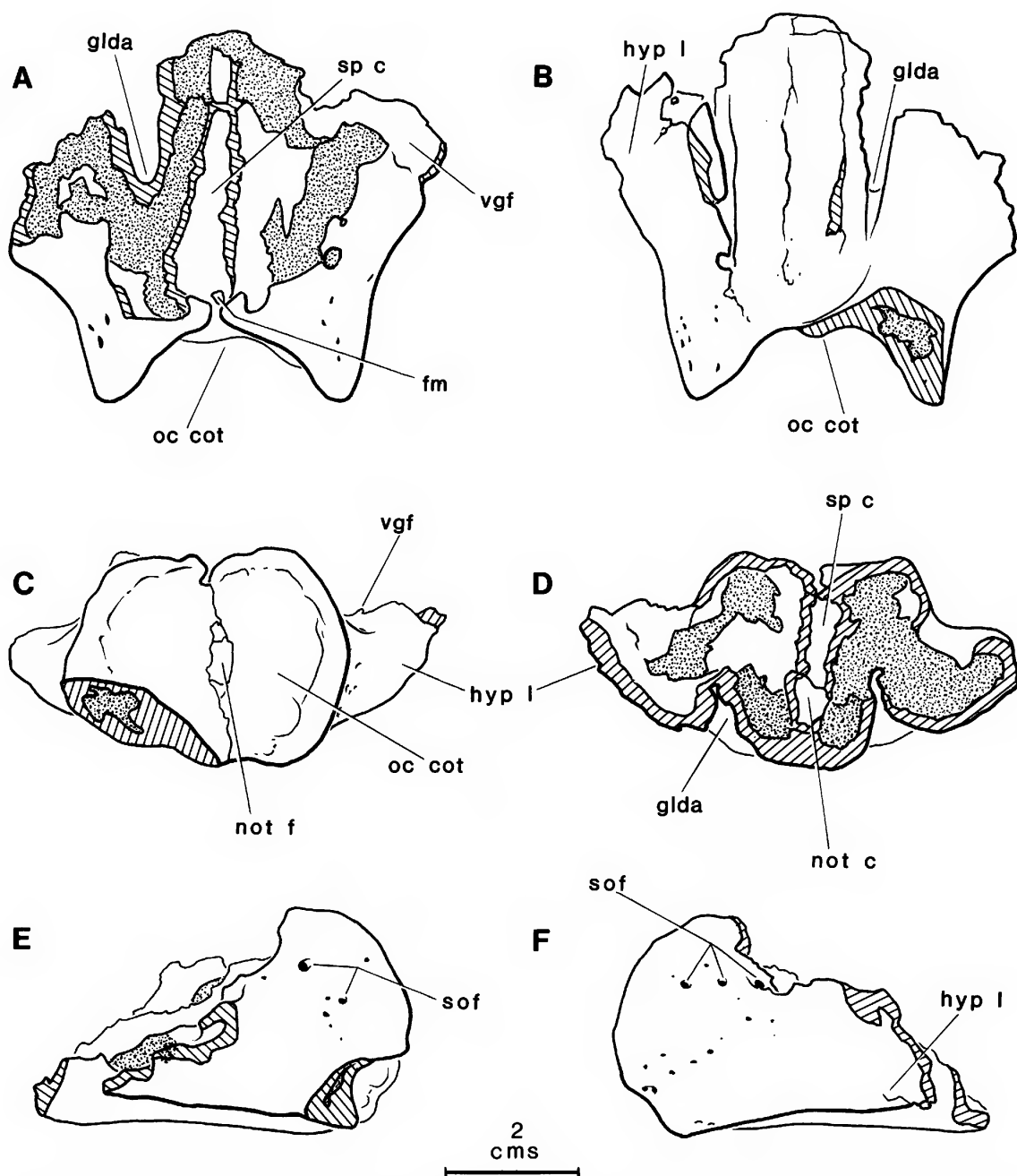


Fig. 5. *Hybodus reticulatus*, BM(NH) P2203D, uncrushed occipital cotylus prepared in acid and associated with a tooth (fig. 10) and two cephalic spines (figs. 12, 13). Occiput shown in (A) dorsal, (B) ventral, (C) posterior, (D) anterior, (E) left lateral, and (F) right lateral views.

holes, separated by a bridge of calcified cartilage, may mark the positions of the optic and trigeminofacialis foramina. Aside from a few foramina for laterosensory innervation through the roof of the orbits, no other open-

ings are evident. If a trigeminofacialis recess was developed as in *H. basanus* and *Xenacanthus*, it has been obliterated during fossilization in P2208, and the postorbital process is crushed down over the posterior part

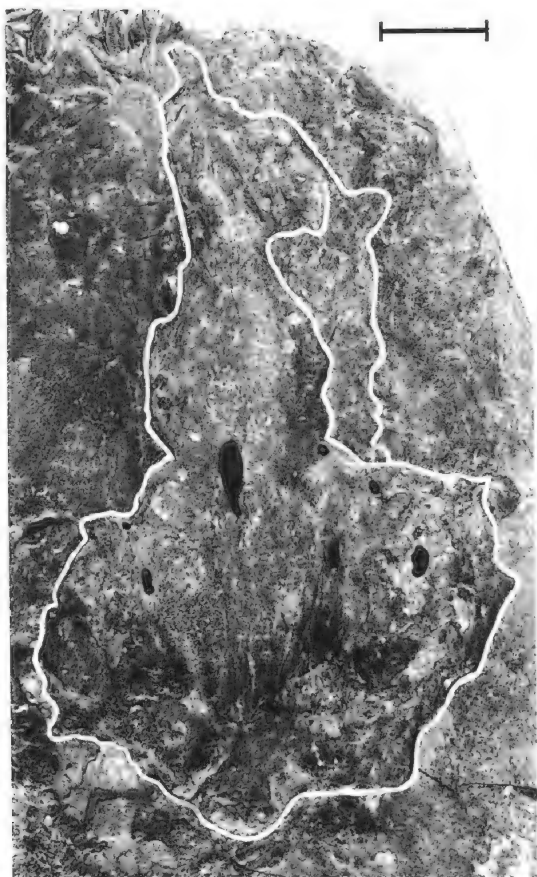


Fig. 6. *Hybodus reticulatus*, BM(NH) P3160, disarticulated braincase (ventral view) and visceral arches. Scale bar = 25 mm.

of the orbit. Nevertheless this at least suggests that the postorbital process of *H. reticulatus* was positioned over any trigeminofacialis region as in *Xenacanthus*, not behind it as in *H. basanus* (see Maisey, 1983, p. 22 and figs. 13, 14). *H. fraasi* resembles *H. basanus* in this respect (Maisey, 1986).

There is a single median foramen for the internal carotids, lying in a shallow depression which also contains a hypophyseal foramen (P3160). The carotid foramen lies approximately level with the efferent pseudobranchial foramina and the posterior limit of the ethmoidal articulation, as in *Xenacanthus* (Schaeffer, 1981, figs. 5, 6). In *H. basanus* the efferent pseudobranchial lies at this level (but farther dorsally), but in *Tamiobatis* and *Cladodus* the internal carotid foramen is located posterior to that of the efferent pseudobranchial.

Paired foramina for the orbital arteries are present in P3160. Their position relative to the median internal carotid foramen is similar to that in *H. basanus*. Shallow grooves for the lateral dorsal aortae extend from the orbital foramina posteriorly and converge toward the occiput. These grooves become much deeper adjacent to the occipital cotylus (P2203d, P3168), and in transverse section the basicranium is interrupted by two deep invaginated clefts within the calcified cartilage (figs. 5, 6).

In modern elasmobranchs the lateral dorsal aorta is entirely superficial to the basicranium, and in some taxa is reduced or even absent, e.g., *Heterodontus*, where the head receives most of its blood via the efferent hyoidean vessel (Maisey, 1982, p. 37). In various Paleozoic elasmobranchs (e.g., "*Cladodus*," *Xenacanthus*, *Tamiobatis*) the lateral aorta would have been enclosed within a prismatically calcified canal for much of its length (Stensiö, 1937; Gross, 1937; Romer, 1964; Schaeffer, 1981). In *Hybodus basanus* there are extremely short bridges of prismatic cartilage enclosing the aortic grooves posteriorly (Maisey, 1982, 1983), but these are lacking in *H. reticulatus* (P2203d and P3168). Deep aortic grooves also occur in *H. hauffianus* (e.g., Brown, 1900, pl. 16, fig. 2; Maisey, 1982, fig. 5). The shape of the basicranium in the occipital region of *H. reticulatus* suggests that strong infolding of the parachordals occurred early in ontogeny, perhaps prior to calcification.

Slightly anterior to the orbital foramen is a smaller one (P3160), comparable to the supposed palatine nerve foramen of "*Cladodus*," *Xenacanthus*, *Tristychius*, and *Hybodus basanus* (Gross, 1937; Dick, 1978; Schaeffer, 1981; Maisey, 1983). This foramen is of uncertain function in the fossils, however, since separate orbital and palatine foramina have been reported in only two Recent elasmobranchs (*Deania*, *Centroscyminus*; Holmgren, 1941) in which the lateral commissure is relatively small and does not enclose the hyomandibular nerve. In *Squatina*, where the lateral commissure is as well developed as in *Hybodus* and many Paleozoic sharks, there is no palatine foramen.

The left postorbital process of P2208 is seen in dorsolateral view, overlain partly by a cephalic spine (figs. 2, 3). The right postorbital

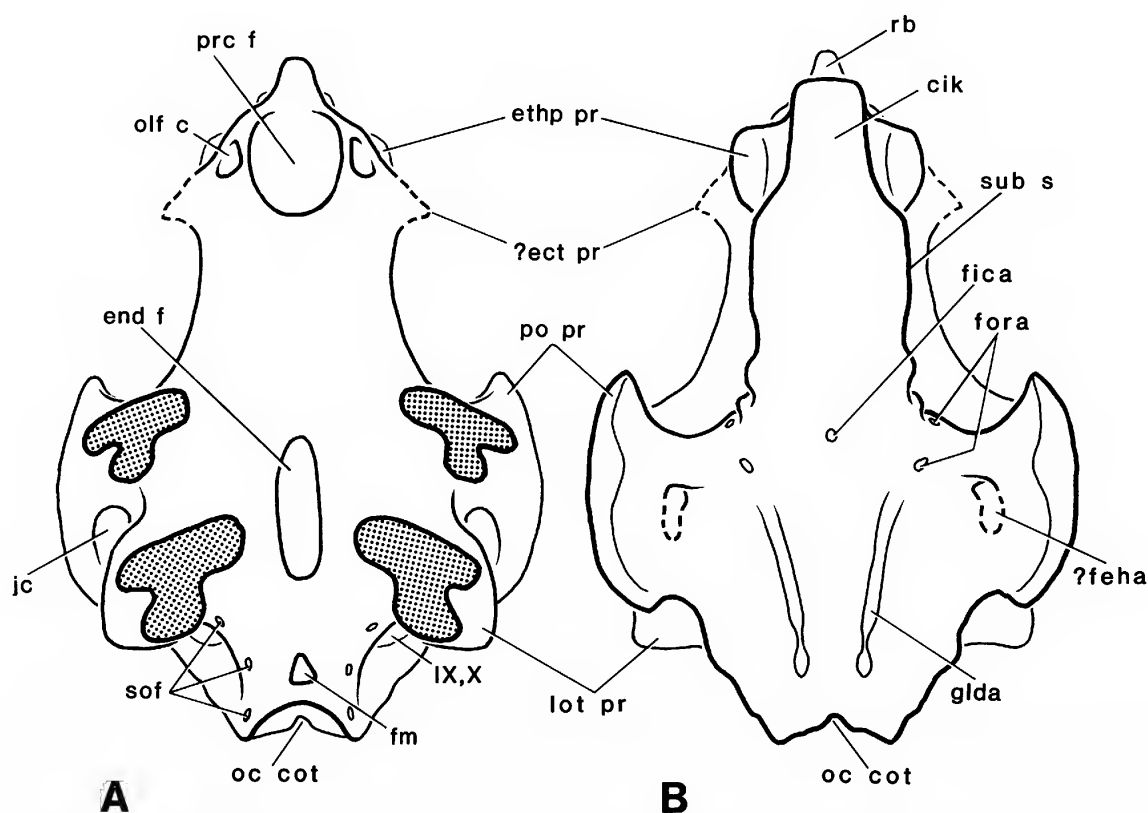


Fig. 7. Outline restoration of the cranium of *H. reticulatus* in (A) dorsal and (B) ventral views; positions of cephalic spines shown stippled.

process of MCZ 816 is preserved but the entire head is covered with shagreen denticles that obscure many details. In P3168 the extreme tip of the right postorbital process is exposed ventrally between the palatoquadrate and ceratohyal. Part of the right postorbital process is preserved in P3160; the floor of the jugular canal has broken away, revealing the roof of this canal. Although broken, the floor of the process was apparently pierced by a large foramen, comparable to the crescent-shaped opening in the postorbital process of *H. basanus* (where it may have housed the efferent hyoidean artery and/or spiracle and/or spiracular organ; Maisey, 1983, p. 26). A similar opening has also been located in the floor of the postorbital process in *H. hauffianus* (Maisey, in prep.).

The postorbital process of *H. reticulatus*, like that of *H. basanus*, is located on the lateral wall of the otic capsule, and is similarly pierced by a wide jugular canal. Distally the process is expanded and flattened where it

overlies the palatoquadrate adductor fossa (P2208, MCZ 816). The hyomandibular head articulates with the otic region behind the postorbital process, but as in *H. basanus* the lateral otic process forms an eave which overhangs the articular region. In P2208 the lateral otic process is shaped so as to articulate with a large dermal cephalic spine. This process and its spine presumably lay directly over the lateral head vein. A comparable arrangement is found in *H. basanus* (P11872). The single pair of cephalic spines in this species corresponds to the posterior pair in *H. reticulatus* and other taxa including *H. hauffianus* and *H. delabechei* (Woodward, 1889b; Brown, 1900; Maisey, 1982). The posterior cephalic spines are slightly larger than the anterior pair (there is a much greater disparity of size in *H. hauffianus*, although the posterior pair is again the larger; Maisey, in prep.). In *H. reticulatus* the anterior (supratemporal) cephalic spine is situated over the posterior part of the orbit. Its base is in contact with the

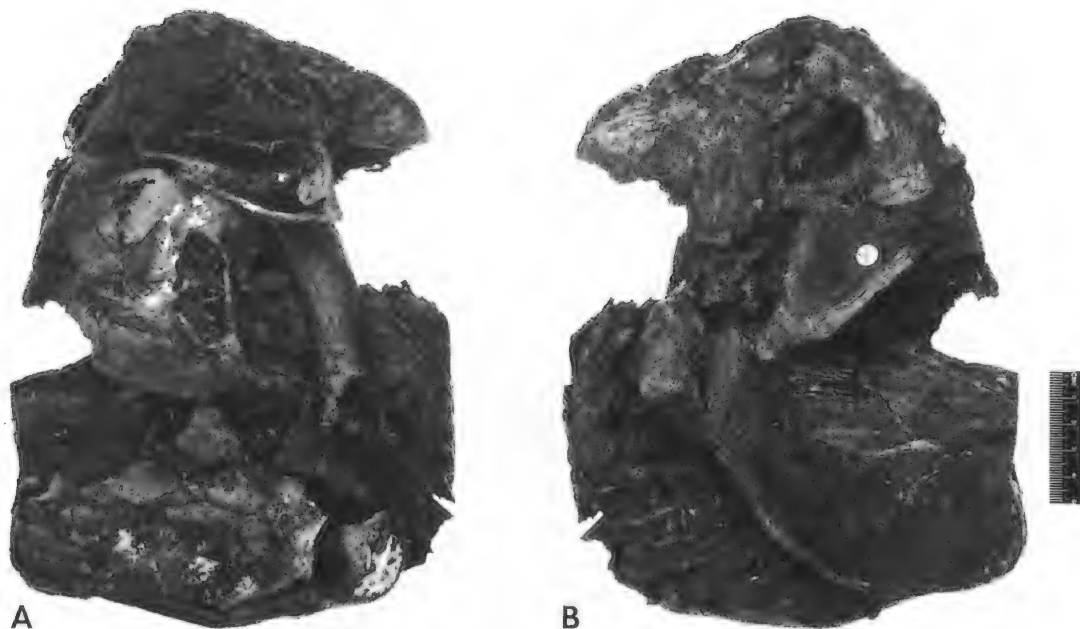


Fig. 8. Indeterminate hybodontid, BM(NH) P50869; (A) left side, showing hyomandibula and ceratohyal plus mesial surface of palatoquadrate and Meckel's cartilage, and oblique view of the floor of the occipital region; (B) right side, showing postorbital process, jugular canal, palatoquadrate (label is on quadrate flange), Meckel's cartilage, end of ceratohyal plus calcified hyoid rays. BM(NH) photos.

supraorbital shelf and the proximal part of the postorbital process in P2208, and there are indications of a very low projection, from the skull roof, upon which the spine rests; this cannot be confirmed from other specimens. A more detailed description of the cephalic spines is given below.

The occiput of P2203d (fig. 5) is 38 mm wide, about 28 mm from top to bottom, and its center (containing the notochordal canal) is approximately 16.5 mm deep (measured from the lateral cotylar projections). The cotylus thus resembles a deep cup. Its inner surface is rugose and pitted, resembling the articular surface of a fossil bone where it would originally have been overlain by a cartilaginous pad. The occiput is calcified (although not prismatically), and is fairly solid, although broken areas of P2203d reveal large internal vacuities and strutlike infoldings of calcified tissue. The floor of the occipital region immediately anterior to the cotylus is prismatic, however, and consists of several

prism layers collectively about 2.5 mm in thickness.

There are at least three ventral spino-occipital nerves in P2203d on the right side, with two preserved on the left, but within the calcified floor of the spinal canal there are several small openings which may indicate an originally greater number of spino-occipital nerves. Six are discernible in BM(NH) P50869, an acid-prepared partial head of an indeterminate Liassic hybodont (fig. 8).

VISCERAL SKELETON

The left palatoquadrate is exposed in lateral view in P2208 (figs. 3, 4). Part of the right palatoquadrate is preserved (covered by shagreen denticles) in MCZ 816. In P3168 the mesial surface of the right palatoquadrate is seen, but the left element is overlain by a mandibular cartilage (fig. 9). Various parts of the palatoquadrate are preserved in other specimens, e.g., BM(NH) 40335, P3160, P3163, P2198a, P2203d, and MCZ 790.

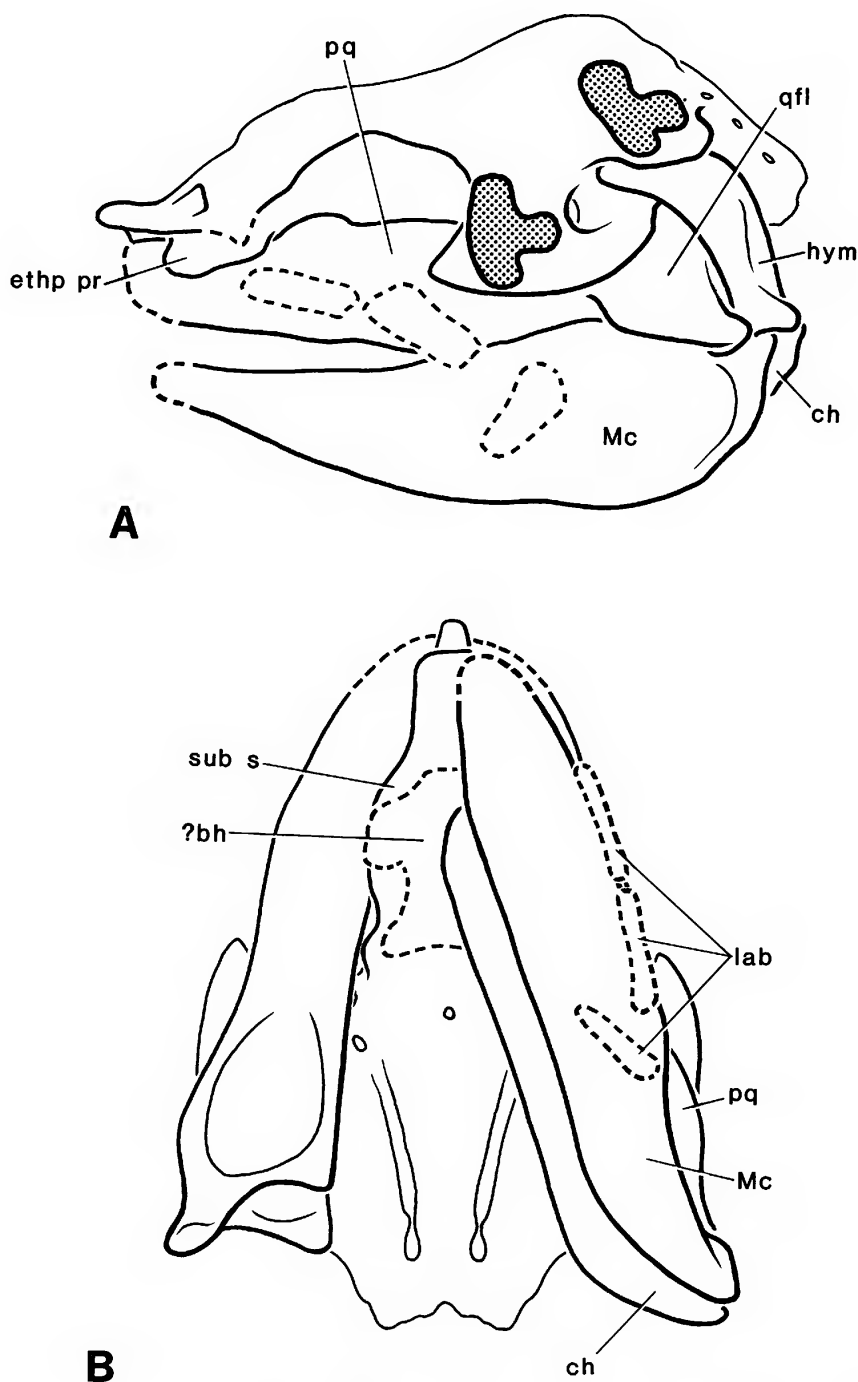


Fig. 9. Restoration of cranium and jaws of *H. reticulatus* in (A) lateral and (B) ventral views; labials and basihyal shown as dashed lines, position of cephalic spines shown stippled.

The palatoquadrate in general resembles that of *H. basanus* in lacking a cleaver-shaped otic process. As in that species, there is a deep adductor fossa defined dorsally by a quadrate

flange, part of which is closely overlain by the postorbital process (P2208; MCZ 816). The posterior margin of the palatoquadrate slopes abruptly toward the articular process,

above which there is a slight concavity to accommodate the hyomandibula. There is no suggestion of a postorbital articulation of the kind found in hexanchoids and many Paleozoic sharks. Instead, there may have been an articulation in the back of the orbit, analogous to the osteichthyan basal articulation. The posterior margin of the suborbital shelf in P3160 bears a pair of oblique ridges and grooves in the region where (in *H. basanus*) the palatoquadrate would leave the orbit and pass beneath the suborbital shelf (fig. 6). This "articular" fold is located on the subocular cartilage (rather than on the interorbital wall as in osteichthyans, where it forms a basitrabecular articulation), suggesting that the "basal" articulation in *H. reticulatus* may be a novel feature, not homologous with that of osteichthyans.

The palatoquadrate ethmoidal articulation is more extensive than in *H. basanus* and *H. fraasi*. There is an articular process on the palatoquadrate, bearing a series of mesial transverse ridges and grooves (P3160). From this process the palatine region tapers toward the symphysis, and its dorsal margin bears a long, narrow articular surface (P2208). In *H. basanus* a corresponding surface articulates with the ventral side of the ethmopalatine process (Maisey, 1982, 1983). The main differences between the palatoquadrates in these species are found in the greater extent of the ethmoidal articulation and the posteriorly indented subocular cartilage of *H. reticulatus*.

Meckel's cartilage is deepest below the center of the palatoquadrate adductor fossa (P2208). It lacks a groove on its lateral surface comparable to the one which contains the anterior lower labial cartilage in *H. basanus* and *H. fraasi*. There are traces of labial cartilages in P2208, but they are poorly preserved. Parts of anterior and posterior upper labials, and traces of a posterior lower labial seem to be preserved. Possibly the labials of *H. reticulatus* were less elaborate than in *H. basanus*, especially in view of the absence of a groove for the anterior lower labial. P2208 suggests that the labials were prismatically calcified, as in *H. basanus*.

Little else can be said concerning the jaws. It is unknown whether the palatoquadrates met symphysially, but the internasal keel of the ethmoid region may have lain between

the palatoquadrates, as in *H. basanus*. A tentative reconstruction of the head with jaws in place is shown in figure 9.

The hyomandibula is visible behind the palatoquadrate of P2208, although its proximal end is overlain by the lateral otic process and its cephalic spine. The distal end of the hyomandibula is blunt, with a shallow concave articulation accommodating the rounded end of the ceratohyal. Both ceratohyals are visible in P3168, together with part of a much-crushed basihyal.

The basihyal of *H. basanus* is characteristically a very bulbous, rounded element with large paired ventral concavities on either side of a narrow median septum (Maisey, 1983, figs. 2, 6, 16, and p. 45). A faintly comparable element in *H. reticulatus* was found after acid preparation of MCZ 780, but is extremely scrappy. It could be interpreted as part of the basihyal but seems to lack bilateral symmetry, and it may instead be the upper (hyomandibular) end of a ceratohyal; it seems too large to be part of a gill arch.

The branchial skeleton is poorly preserved in all the available material. In P3168 there are traces of five arches (represented by ceratobranchials) anterior to the scapulocoracoids (fig. 4). Additionally, what may be part of a basibranchial copula lies across the basicranium, behind the right ceratohyal. There are five branchial arches in *H. basanus* (Woodward, 1889a, p. 274; 1916, p. 8; Maisey, 1982, p. 15; 1983, p. 47), but nothing is known of its basibranchial skeleton. In P2208, three or four epibranchials and parts of two or three pharyngobranchials are discernible (figs. 2, 3), but they are too badly damaged for comparative purposes. Pharyngobranchials have been noted in *H. hauffianus* (Koken, 1907) and *H. cassangensis* (Maisey, 1982). Epibranchials are known in these species and in *H. basanus* (Woodward, 1916; Maisey, 1983).

DERMAL SKELETON

1. **TEETH:** *Hybodus reticulatus* is recognized primarily by its tooth morphology (Agassiz, 1837, p. 178; Woodward, 1889a, p. 266; 1916, p. 4; see diagnosis given earlier). The present account relies heavily on a hypodigm of several specimens (including one of the originally figured pieces). All of these

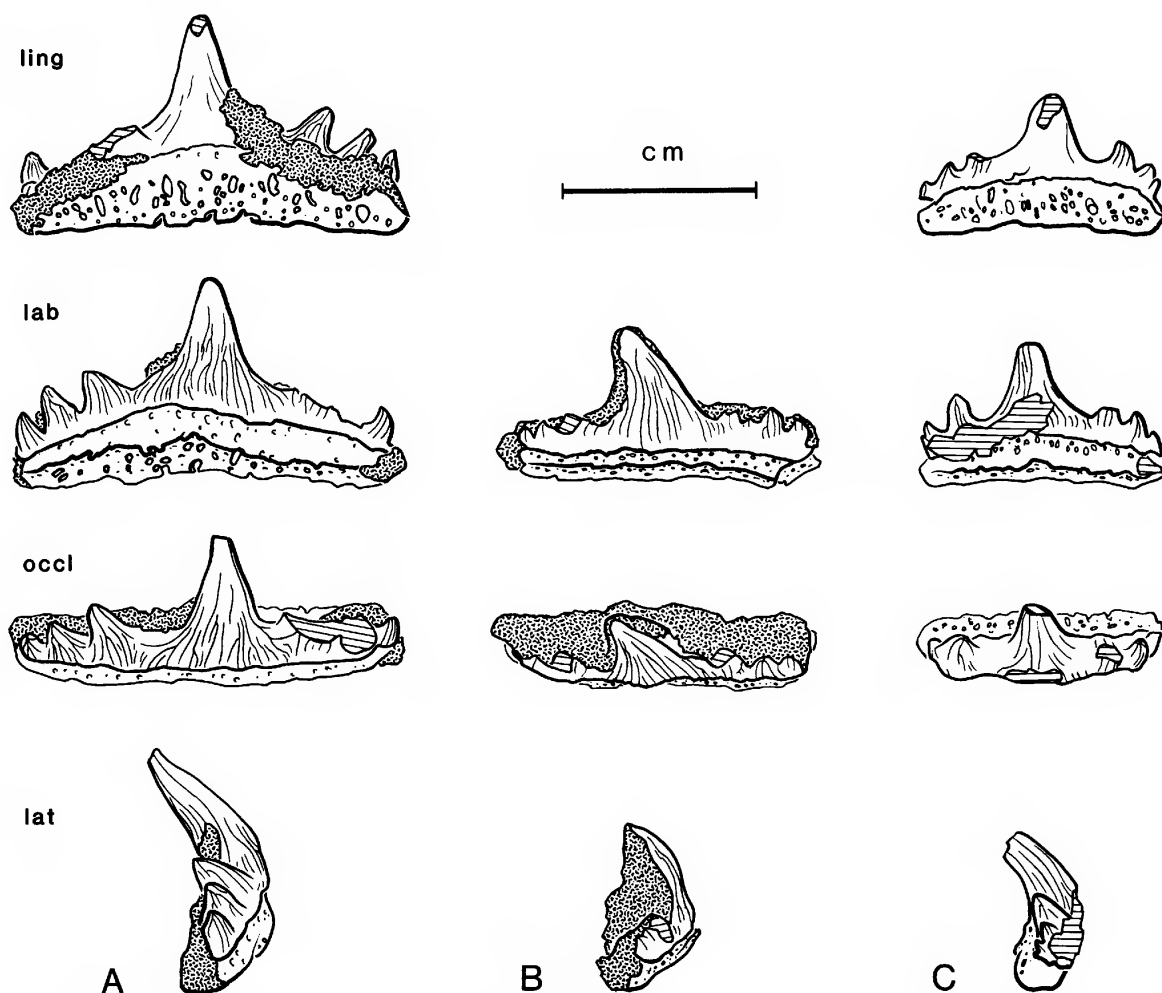


Fig. 10. Teeth from some *H. reticulatus* specimens; (A) MCZ 780, (B) MCZ 816, (C) BM(NH) P2203D. Scale bar = 10 mm.

are identified on the basis of associated teeth, some of which are illustrated here (figs. 1, 2, 10). None of the specimens is sufficiently intact to establish the range of dental variation and number of tooth rows as completely as in *H. basanus* (Maisey, 1983, figs. 19, 20).

A broken tooth from BM(NH) P2203d was subjected to SEM (scanning electron microscope) examination in order to determine the enameloid ultrastructure in *H. reticulatus* (fig. 11). The area shown in figure 11A is from a large lateral cusp next to the principal one. The ridge crossing the upper part of figure 11A is one of the longitudinal striae ornamenting the accessory cusp. Figure 11B shows the area outlined in figure 11A at higher magnification. The etched surface reveals a layer

of single crystallite enameloid (SCE), confirming Reif's (1973) suggestion (founded on observations of other *Hybodus* spp. teeth) that this type of enameloid is typical of *Hybodus*. There is no indication of parallel-fibered or haphazardly fibered enameloid layers. The single-crystallite enameloid of *H. reticulatus* is very similar to that described in *H. delabechei* by Reif (1978a, fig. 7b), with vertically oriented crystallites except at the very surface of the tooth. SCE seems most parsimoniously to be a primitive character among Hybodontidae. By contrast, the "triple-layered" enameloid of modern elasmobranchs (Reif, 1973) is almost certainly a derived condition (Reif, 1978a; Duffin, 1981; Thies, 1982; Duffin and Ward, 1983; Maisey, 1984a, 1984b). Some

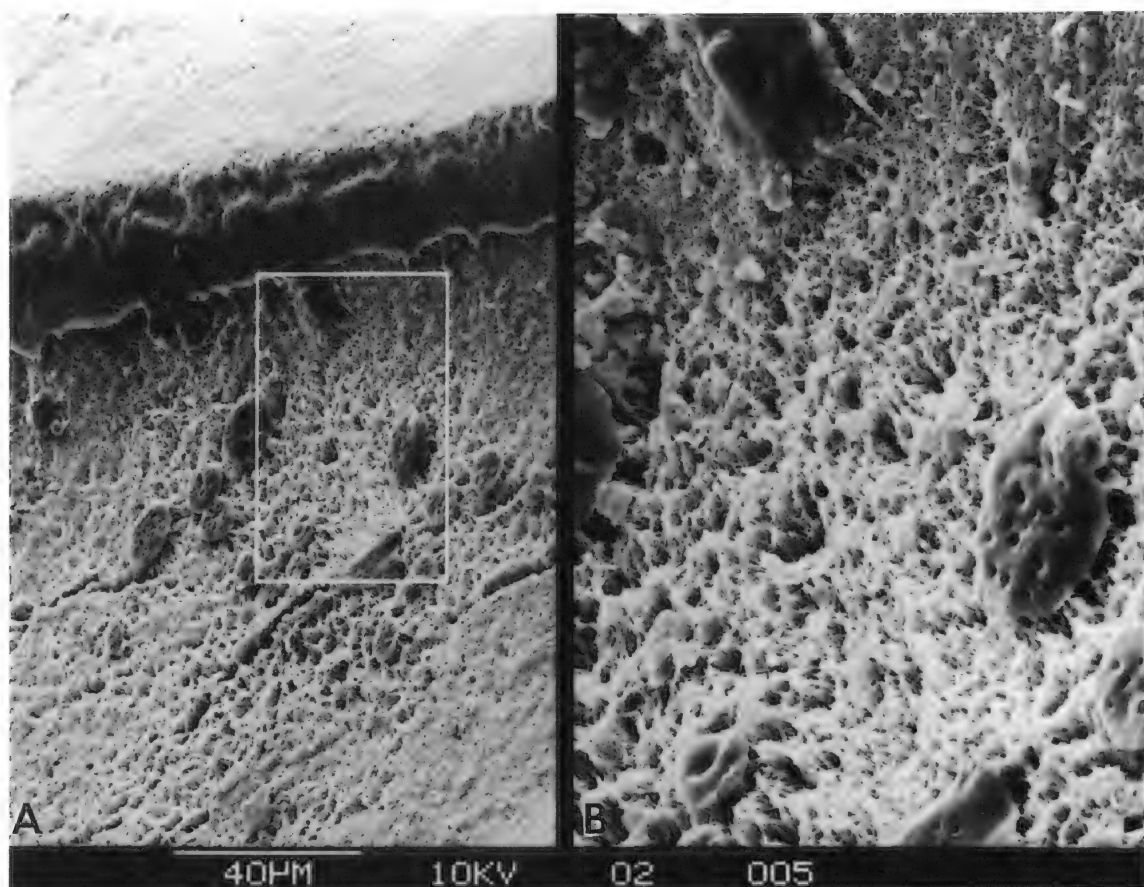


Fig. 11. Tooth enameloid ultrastructure in *H. reticulatus*, from a broken tooth of BM(NH) P2203D, etched in 2 N HCl for 5 seconds, gold-coated, and photographed using a Cambridge Stereoscan 250 at 10 kV. See text for details.

fossils previously thought to be Hybodontidae (e.g., *Synechodus*, *Palaeospinax*) also have “triple-layered enameloid” (Reif, 1973, 1978a), which (together with various other skeletal and dental characters) distinguishes them as primitive neoselachians (Maisey, 1975, 1977, 1984a, 1984b, 1985; Duffin and Ward, 1983).

The tooth crown of *H. reticulatus* is composed largely of trabecular osteodentine (Agassiz, 1837, pl. M₁, fig. 5). Osteodont histology is of fairly restricted distribution in shark teeth; it has been identified in *Hybodus* and *Acrodus* spp., but not in all other Hybodontidae. In this regard, it is important to note that the crowns of teeth generally referred to *Polyacrodus* are orthodont (e.g., Patterson, 1966, pl. 5, fig. 1), whereas many Hybodontidae such as *H. hauffianus* possess

osteodont teeth, as in *H. reticulatus*. Jaekel’s (1898, 1906, 1911) notion that *H. hauffianus* should be referred to *Polyacrodus* (and that *Hybodus* be relegated to the status of a fin-spine form genus, which has been vigorously disputed, e.g., Koken, 1907; Stensiö, 1921) now seems to be without foundation. Tooth morphology is discussed further below (see Comments, Section 3).

2. DERMAL DENTICLES: Dermal denticles cover much of the head in MCZ 816. Simple unicuspid scales and multicuspid compound scales are both present, the latter especially around the mouth. Over most of the head the denticles are under 1 mm diameter, but larger denticles (1.5–2+ mm diameter) occur near the snout, dorsally above the occiput, and in a patch above the rear of the orbit (where there is an anterior cephalic spine in males).

According to Woodward (1889b), compound scales occur only behind the head in *H. delabechei*, but this is not true of all specimens (Reif, 1978b). In that species the denticles are slightly larger dorsally and anterior to the orbits and there is also a mixture of compound ("growing") and unicuspid ("non-growing") scales (Reif, 1978b). In *H. basanus* only unicuspid scales occur on the head (Maisey, 1982, 1983), and in *H. fraasi* such scales are present over the entire body, no compound scales having been found (Maisey, 1986).

As Reif (1978b, p. 120) found in *H. delabechei*, the compound "growing" scales of *H. reticulatus* have a low cusp count (generally only two or three), suggesting that few odontodes were involved in forming each denticle and that even these "growing" denticles were periodically shed. In general, the simple unicuspid scales of *H. reticulatus* are tumid and blunt, whatever their size, and would have formed a rugose covering to most of the head. The multicuspid scales are mostly acuminate, with sharply pointed cusps. Similar (but unicuspid) denticles fringe the mouth in living *Chlamydoselachus* where they take on an almost toothlike appearance (Garman, 1885, pl. VI, fig. 12). Examination of cleared and stained 175 mm and 205 mm *Chlamydoselachus* embryos (personal observ.) shows that the first unicuspid tooth generation is followed by replacement teeth having two or three acuminate cusps which may have secondarily fused together, although it cannot be determined from the available material whether pre- or postpapillary concrescence has actually occurred.

3. CEPHALIC SPINES: Cephalic spines of *H. reticulatus* are of two sizes. The terminology used in this description is taken from Maisey (1982). The anterior (supratemporal) pair is slightly smaller than the posterior (supraotic) pair. In BM(NH) P2208 the left supratemporal and both supraotic spine bases are preserved in situ, but their crowns are missing (figs. 2, 3). In P2203d, two almost complete cephalic spines of different sizes (presumed to be the right supratemporal and supraotic spines) have been acid prepared from the matrix (figs. 12, 13).

The supratemporal spine of P2203d is 33.5 mm wide, 21.5 mm long, and is 21 mm high

(height measured vertically from the center of the basal platform; fig. 12). The posterior lobe of the basal platform is 10.5 mm wide and extends posteriorly about 9 mm from the crown base. There is a "gum-line" extending approximately 2 mm from the crown base laterally and posteriorly but not anteriorly. The lateral lobe projects almost 11 mm, and the mesial lobe about 12.5 mm from either side of the posterior lobe. The mesial and lateral lobes are slightly oblique, so that the mesial marginal indentation is more acute than the lateral indentation. Both indentations are deep, giving the basal platform a strongly triradiate appearance. The crown consists of a principal retrorse cusp with a weak apical barb posteriorly. The barb is joined to the cusp apex by a posterior crest, and a nearly straight mesial crest extends obliquely across the curved crown from the barb toward the basal platform. Numerous weak striae branch from this crest proximally, and the crest disappears among several stronger proximal crenulations about 5 mm from the base. A laterally displaced "dorsal" crest extends from near the apex toward the base, also disappearing among the basal crenulations about 3 mm from the base. Unlike the mesial crest, however, the dorsal crest does not give off any striae.

The supraotic spine of P2203d is 38 mm wide, 26 mm long, and approximately 28 mm high (fig. 13). The posterior lobe is slightly more than 11 mm across and projects posteriorly about 15 mm. Its "gum-line" is almost 4 mm deep posteriorly. The lateral and mesial lobes both project approximately 13.5 mm. Lateral and marginal indentations are deep. The barbed crown has a weak mesial crest, a stronger posterior crest, and a dorsal crest that is prominent only near the apex, then becomes faint and indistinct proximally. There are several proximal wrinkles anteriorly, but these are weaker and not so rectilinear as on the suprapostorbital spine.

Both spines have small, rounded accessory cusps flanking the main one. In both spines the mesial accessory cusp is more prominent, and on the supratemporal spine the mesial accessory cusp bears a few striae. The basal platforms are typically spongy and porous. They lack any ordered pattern of canals or foramina, but there are one or two larger

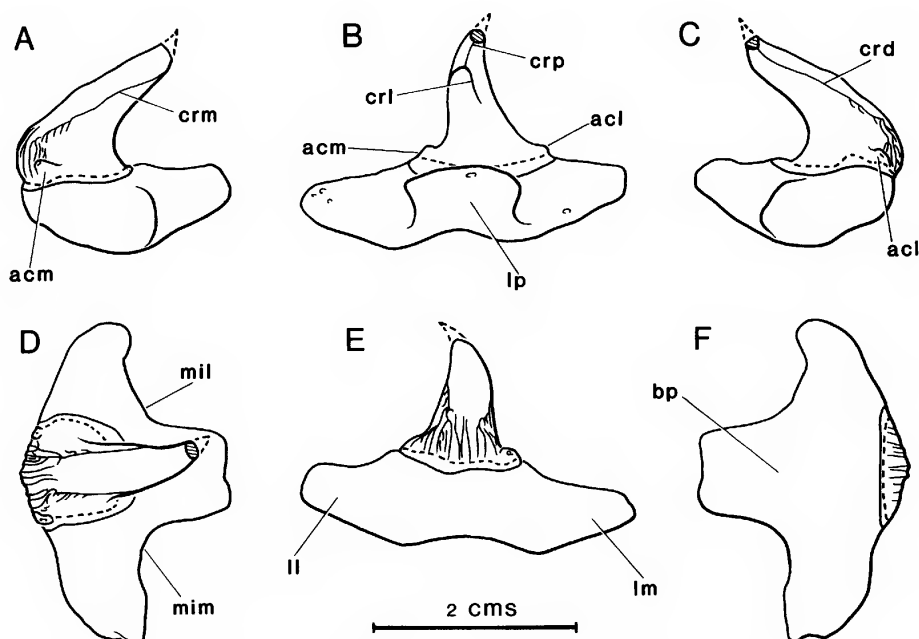


Fig. 12. Smaller cephalic spine of BM(NH) P2203D; comparison with BM(NH) P2208 suggests this is the right supratemporal spine. Views are of (A) mesial, (B) posterior, (C) lateral, (D) dorsal, (E) anterior, and (F) ventral aspects.

openings (e.g., on the dorsal side of the posterior lobe of the supratemporal spine, fig. 12).

For comparison, the following measurements were obtained from P2208; left supratemporal spine 28 mm wide, 16.5 mm long, maximum width of posterior lobe 12.5 mm, mesial lobe projects 11 mm, lateral lobe 7.5 mm; left supraotic spine 32 mm wide, 19.5 mm long, maximum width of posterior lobe 15 mm, mesial lobe projects 11.5 mm, lateral lobe 11.5 mm. From this it appears that P2203d represents a much larger individual than P2208. This is supported by tooth size; although those of P2203d are from an unknown position in the mouth, they are rather squat anterior teeth. One of these (fig. 10C) measures 13.5 mm across, whereas the largest lateral tooth visible in P2208 is only 14.5 mm across, and its anterior teeth are generally less than 9 mm across.

In *H. reticulatus* the supraotic cephalic spines occupy the same topographic position as the single pair in *H. basanus* (Maisey, 1982, fig. 15), and it would seem that the supratemporal pair is absent in that species. In *H.*

delabechei there are two pairs, arranged as in *H. reticulatus* (Woodward, 1889a, pl. 8, fig. 1; Maisey, 1982, figs. 3B, 15C). There are two pairs in *H. hauffianus* (Brown, 1900). As far as can be determined, the supraotic pair is arranged as in *H. reticulatus* and *H. delabechei*, but the supratemporal spines lie closer together (Maisey, 1982, fig. 15B). Two different-size pairs of cephalic spines have also been found in *Acrodus lateralis* (Rieppel, 1981).

The arrangement of cephalic spines can be studied in only a handful of specimens, and consequently the extent to which spine morphology varies, both between and within taxa, is largely unknown. The principal morphological features of cephalic spines have been described by Maisey (1982, p. 29, figs. 15, 16), who also identified several asymmetrical characteristics which may be useful in distinguishing between left and right antimeres. These characteristics include striation patterns on the principal cusp and the asymmetrical shape of the basal plate. Investigation of the cephalic spines in *H. reticulatus* partly corroborates these earlier suggestions

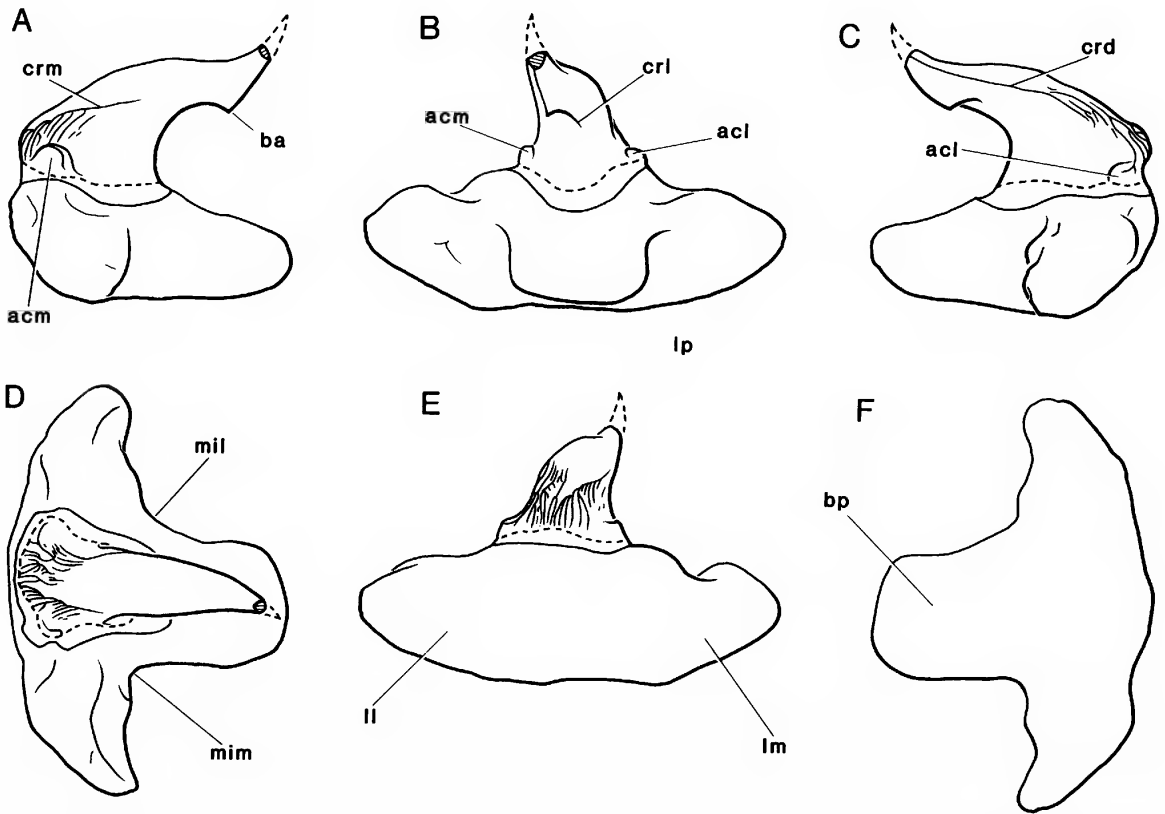


Fig. 13. Larger cephalic spine of BM(NH) P2203D; comparison with BM(NH) P2208 suggests this is the right supraotic spine. Views are as in figure 12, and are to same scale.

concerning spine asymmetry. Asymmetrical features of the principal cusp (e.g., laterally offset dorsal crest; mesial crest meets posterior crest at barb apex; lateral crest very short) are consistent among those taxa investigated (*H. reticulatus*, *H. delabechei*, *H. hauffianus*, *H. basanus*, *Asteracanthus ornatissimus*). There seems to be less consistency in the asymmetry of the basal plate, however. As Maisey (1982) has noted, some cephalic spines have an almost bilateral symmetry (e.g., Woodward, 1916, pl. 1, fig. 4; Patterson, 1966, fig. 26B; Cappetta and Case, 1975, pl. 1, figs. 3–6). Comparison of cephalic spines of *Asteracanthus ornatissimus* (e.g., BM(NH) P12522; Maisey, 1982, fig. 46A–F) and *Hybodus reticulatus* (figs. 12, 13) reveals that, according to the asymmetrical features of the crown, the basal plate's "lop-sidedness" is reversed. Since the basal plate is closely attached to special areas on the skull roof, this plasticity in spine asymmetry suggests that

there is greater corresponding morphological variation in the skull roof of Hybodontidae than is presently recognized.

A further note may be added concerning the accessory (lateral and mesial) cusps of hybodontid cephalic spines. These are lacking in many Cretaceous examples, including *H. basanus* (Woodward, 1916, pl. 1, figs. 2, 2a; Maisey, 1983, fig. 24) and specimens referred to *Lonchidion* (Estes, 1964; Patterson, 1966), as well as in Jurassic *Asteracanthus* (Woodward, 1888, pl. 12, figs. 7, 8; Maisey, 1982, fig. 16A–F). Woodward (1889b, p. 260) noted that in a specimen of *H. delabechei*, BM(NH) 39880, the posterior (supraotic) cephalic spines lack accessory cusps, while the anterior (supratemporal) ones possess them. In *H. basanus*, the single pair of cephalic spines (which are topographically equivalent to the supraotic pair in other hybodonts) also lacks accessory cusps. Both of the associated *H. reticulatus* cephalic spines, preserved in



Fig. 14. *Hybodus* cf. *reticulatus*, BM(NH) P5880, Upper Lias, Boll. Württemberg; disarticulated visceral arches, teeth, and ?cranium.

BM(NH) P2203d, have accessory cusps on either side of the principal one, although in neither example are the accessory cusps more than low, tumid lobes. In BM(NH) P2208 the bases of both supraotic spines and the left supratemporal spine are preserved in situ. None of the crown is preserved on the supratemporal spine, but there are traces of accessory cusps adjacent to the base of the principal one. Therefore it is concluded that the absence of accessory cusps is not a reliable means of distinguishing supraotic from supratemporal cephalic spines. However the possibility remains that the relative development of these accessory cusps is of taxonomic value among various Hybodontidae, despite the paucity of data at present.

There are no indications of incremental growth of *H. reticulatus* cephalic spines externally or from histological sections (e.g., Agassiz, 1837, pl. M₂, figs. 1–3). We may surmise that hybodontid cephalic spines were periodically shed and replaced by new, larger ones. This process would not have been continuous, unlike tooth or denticle replacement,

otherwise spines of gradational sizes would probably be found on individual males (analogous to the bizarre presence of several caudal spines of differing sizes in some sting rays). However the periodicity (if any) is unlikely ever to be determined. The possibility is raised that some incomplete “female” hybodontid specimens lacking cephalic spines are simply immature males, or the elasmobranch equivalent of a stag in winter. In smaller cephalic spines the principal cusp has an open pulp cavity, but in larger specimens this is filled in, usually by concentric orthodontine lamellae. This suggests that these spines were retained for an appreciable time before being lost.

4. FIN SPINES: The apex of a dorsal fin spine is preserved in P2208 (figs. 2, 3). It bears several longitudinal ribs, and has retrorse denticle rows posteriorly (see Maisey, 1978, for terminology). There are no distinctive features to separate the spines of *H. reticulatus* from those of some other Hybodontidae such as *Acrodus* or *Palaeobates*. The specimens described by Agassiz (1837, p. 180, pl.

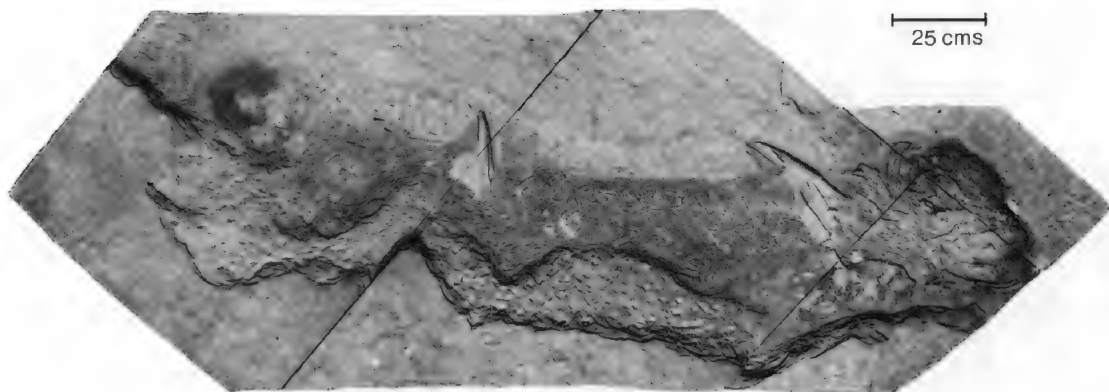


Fig. 15. *Hybodus* cf. *reticulatus*, SMNS 51949, almost complete specimen lacking tail.

24, fig. 26, pl. 22a, figs. 22, 23) and Woodward (1889a, p. 267) are regarded here as specifically indeterminate.

Hybodus cf. *reticulatus*

REFERRED MATERIAL:

BM(NH) P5880, Upper Lias, Boll, Württemberg, large slab with disarticulated elements of the jaws, hyoid and visceral arches, teeth, fin spine, and possibly parts of the braincase.

SMNH 51949, Upper Lias, Schwarzjura Eile, Holzmaden, Württemberg, coll. G. Fischer, 1980, almost complete specimen, preserved length approx. 2 m, lacking caudal fin.

A detailed revision of Upper Liassic Hybodontidae from Württemberg, Germany, is in preparation, and it would be premature to discuss them in detail here. Two specimens deserve mention at this point, however, as their tooth morphology resembles that of *H. reticulatus* rather more than *H. hauffianus* from the same locality. One of these specimens, BM(NH) P5880, from Boll (Woodward, 1889a, p. 268) is poorly preserved and lacks a braincase (fig. 14). The other specimen, recently collected at Holzmaden (SMNS 51949), is more complete than P5880, and has been extensively prepared (figs. 15, 17). Its teeth are multicuspoid, with gracile acuminate cusps which are striated proximally (those of *H. hauffianus* are generally less acuminate and more completely striated; Fraas, 1896). Teeth in the BM(NH) example are poorly exposed and it is not therefore pos-

sible to make as detailed a comparison as one would like (fig. 16).

The dorsal surface of the braincase is exposed in SMNS 51949, but only the posterior portion (as far forward as the postorbital process) can be discerned. The arrangement of the occiput, otic capsules, lateral otic process, and postorbital process is as in *H. reticulatus*, *H. hauffianus*, and *H. basanus*. The basicranium and ethmoidal region are not exposed in SMNS 51949, and only fragments of the occiput are visible in BM(NH) P5880. Specimens of *H. hauffianus* from Holzmaden possess a broader internasal keel than *H. reticulatus* from England (which, in turn, has a wider internasal keel than *H. basanus*; see above), so it would be interesting to compare this feature in *H. cf. reticulatus* from Germany. The neurocranium of SMNH 51949 features broad supraorbital crests, but the left postorbital process is missing and the right one is overlain by visceral arch elements (ceratohyal, Meckel's cartilage), so the dorsal outline of the braincase does not entirely reflect its original shape (fig. 17).

The upper and lower jaws are preserved in both specimens. Their overall morphology is similar to that found in *H. reticulatus* from England. The palatoquadrate of SMNH 51949 has a broad but low "palatine" process, as in BM(NH) P2208. This process is more prominent in adult *H. hauffianus* (Koken, 1907; Maisey, 1982), but in BM(NH) P3168, a small (juvenile?) specimen of *H. reticulatus*, the process is also well developed.

The hyomandibula and ceratohyal of SMNH 51949 are shaped as in *H. reticulatus* (BM(NH) P2208-P3168) and *H. basanus* (Maisey, 1982, 1983). The ceratohyal bears a deep fossa at its posterior end, as in *H. basanus* and *Xenacanthus* (Maisey, 1983, p. 45), perhaps for an *adductor hyomandibularis* muscle (no such muscle occurs in Recent chondrichthyans, according to Edgeworth, 1935).

In the absence of conflicting evidence, therefore, the Holzmaden fauna seems to include *H. reticulatus* or at least a very closely related species, and *H. reticulatus* may consequently range from the Lower to the Upper Lias.

SOME COMMENTS ON HYBODONTID PHYLOGENY AND TAXONOMY

1. COMPARISON OF *H. RETICULATUS* AND *H. BASANUS*

From the preceding description it is possible to determine that the cranial anatomy of *H. reticulatus* closely resembles that of *H. basanus*, and that together these taxa differ from Recent elasmobranchs in several respects (see also Maisey, 1982, 1983). Some of these differences probably represent apomorphic characters (or character states) of Recent elasmobranchs, including the arrangement of subcranial arteries; lack of an ethmoidal keel; generally uncalcified lateral commissure and unenclosed jugular canal (cf. *Squatina*, however); the relative positions of occiput and otic capsules; the presence of calcified centra (including an occipital half-centrum in Recent sharks); and closure of the adult hypophyseal foramen (see Maisey, 1982, p. 36; 1984a). Other features have been considered apomorphic for *Hybodus* and a few other genera (e.g., *Acrodus*, *Lissodus*, *Asteracanthus*, *Palaeobates*; Maisey, 1982, p. 40). Among those characters, the following are known to be shared by *H. reticulatus* and *H. basanus*:

- a. large, downturned postorbital processes,
- b. inflated and long jugular canal,
- c. massive ethmopalatine process ventral to olfactory canal,
- d. lateral commissure broadly plastered on lateral surface of otic capsule,

- e. lateral otic process positioned immediately behind and in part dorsal to postorbital process,
- f. large, well calcified labial complex,
- g. palatoquadrate with elongate and deep adductor fossa overlain by quadrate flange, no postorbital articulation, but with an elongate ethmoidal articulation extending from the rostral bar to the orbitonasal lamina,
- h. hyomandibula located in part dorsal to the palatoquadrate,
- i. shagreen and oropharyngeal denticles with several "neck" canals, but lacking a strong constriction between base and crown,
- j. fin-spine morphology (see Maisey, 1978),
- k. teeth lacking specialized nutritive foramina ("anaulacorhize" condition; Casier, 1947c, p. 6),
- l. "*Sphenonchus*" cephalic spines present (in males).

Hybodus reticulatus differs from *H. basanus* in having:

- m. longer rostral bar,
- n. larger and stronger ethmoidal articulation,
- o. broader internasal keel,
- p. olfactory capsule with a calcified mesial wall,
- q. efferent pseudobranchial foramen located farther ventrally,
- r. postorbital process overlying trigemino-facialis region,
- s. anterior paired cephalic spines present,
- t. deeper grooves for lateral aorta, with no posterior bridge of calcified cartilage,
- u. higher number of spino-occipital nerves,
- v. folds in subocular cartilage to accommodate palatoquadrate in rear of orbit,
- w. no groove on Meckel's cartilage for an anterior labial,
- x. compound ("growing") dermal denticles.

Some of these differences (e.g., characters p, u) may be trivial (such variations being common among Recent elasmobranchs), and others (e.g., character q) might be artifacts due to preservational differences. Many more seem to be primitive attributes of *H. reticulatus* (suggested by comparison with other hybodontids, *Xenacanthus*, *Tamiobatis*, *Ctenacanthus*, *Cladoselache*, *Hopleacanthus*,

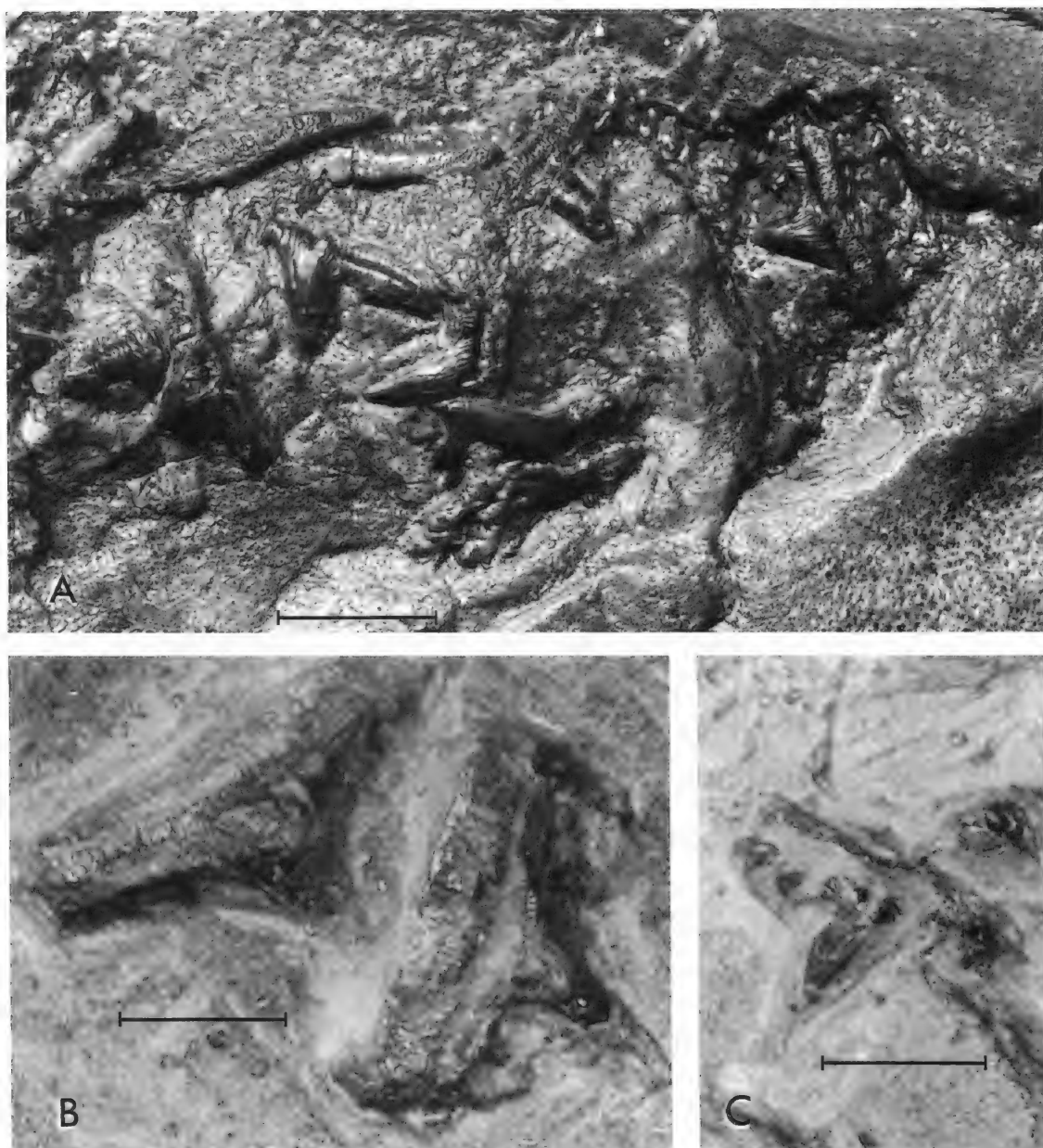


Fig. 16. Teeth from (A) SMNS 51949, (B, C) BM(NH) P5880. Scale bar = 10 mm.

“*Cladodus*,” *Cobelodus*, *Tristychius*, and *Onychoselache*), including m-o, r, t, w, x. *Hybodus basanus* is therefore distinguishable from *H. reticulatus* in the following presumably apomorphic features:

1. short rostral bar
2. shortened ethmoidal articulation
3. narrow internasal keel
4. trigeminofacialis fossa not overlain by postorbital process
5. suprapostorbital cephalic spines absent
6. shallow grooves for dorsal aorta
7. groove in Meckel's cartilage for anterior lower labial cartilage
8. absence of “growing” dermal denticles

The holotype (and still the only example) of *Hybodus fraasi* in Munich agrees with *H. basanus* in characters 1, 2, 4, 7, and 8 (remaining features unknown in *H. fraasi*; Maisey, 1986). These similarities suggest that an

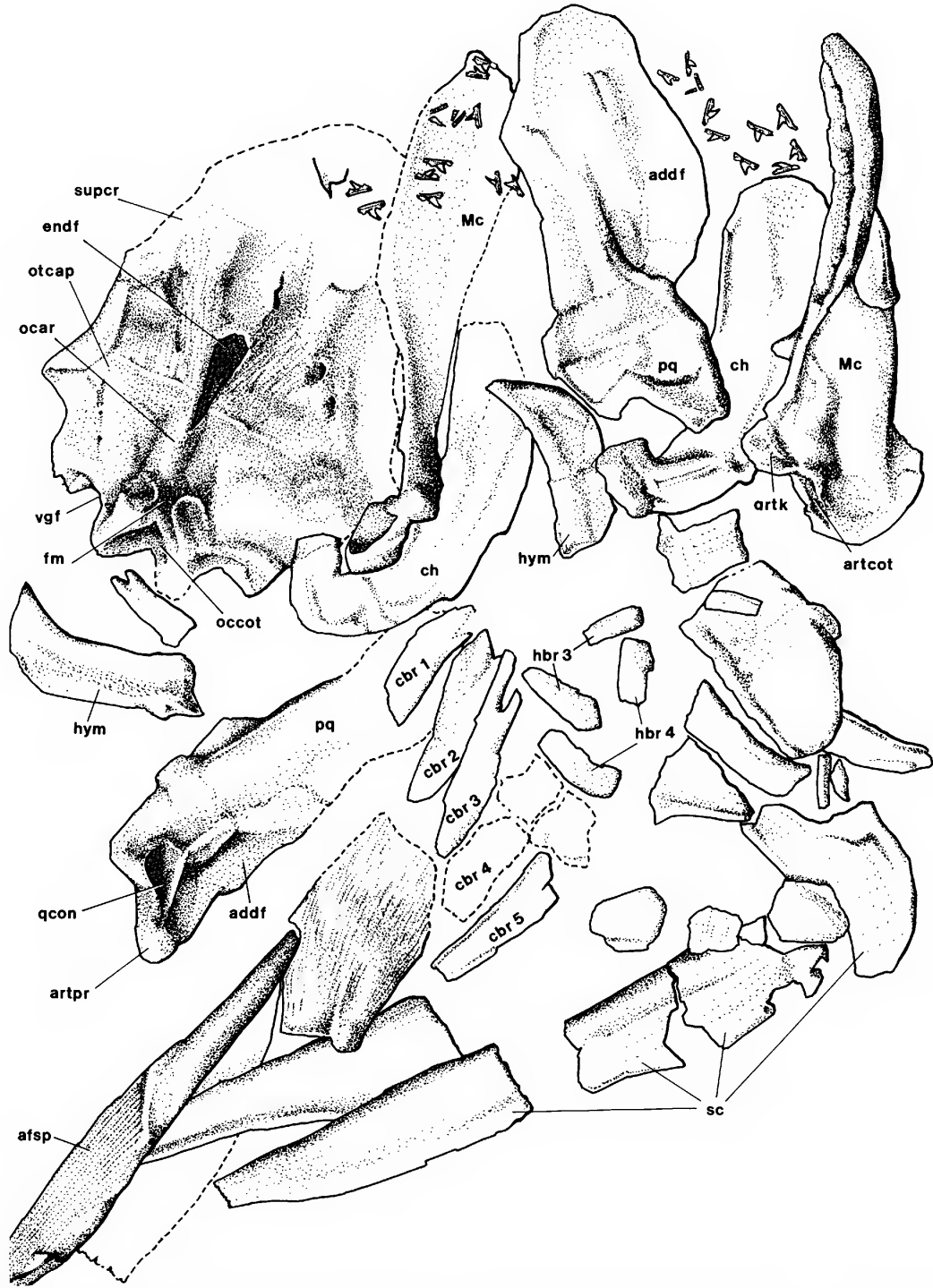


Fig. 17. Head of SMNS 51949 showing principal elements of cranium (in dorsal aspect), disarticulated jaws and hyoid arch, ventral elements of the branchial arches, scapulocoracoids, and fin spine.

advanced group, represented by *H. basanus* and *H. fraasi*, can be distinguished from more

generalized Hybodontidae, but *Hybodus* itself remains poorly diagnosed. The genus may

be derived in lacking any calcified bridge over the dorsal aortic grooves, and possibly in possession of subocular folds in the rear of the orbit, but it must be admitted that at present these characters do not provide a substantial or particularly useful diagnosis. As defined above, the family Hybodontidae includes many nominal species of *Hybodus*, some of which cannot be distinguished above the species level from *H. reticulatus*, plus a few derived species (e.g., *H. basanus*, *H. fraasi*) distinguishable on the basis of several non-dental characters. To make the classification reflect this phylogeny, I propose the erection of a new genus to separate *H. basanus* and *H. fraasi* from *H. reticulatus*.

Egertonodus, new genus

DIAGNOSIS: Hybodontidae with ethmopalatine articulation extending only onto the anterior part of orbitonasal lamina; trigeminofacialis fossa not overlain by postorbital process; shallow grooves for lateral dorsal aortae; single (posterior) pair of cephalic spines; only nongrowing dermal denticles on body and in oropharynx; groove on Meckel's cartilage for anterior lower labial cartilage; multicuspoid osteodont teeth.

ETYMOLOGY: Named after Sir Philip Egerton, who first described the type species.

TYPE SPECIES: *Egertonodus basanus* (Egerton). [*Hybodus basanus* Egerton, 1845, p. 197, pl. iv.] Note: see Maisey (1983) for list of citations and for details of the cranial anatomy in this species.

OTHER REFERRED SPECIES: *Egertonodus fraasi* (Brown). [*Hybodus fraasi*, Brown, 1900, p. 151, pl. xv, fig. 1.] Note: The assignment of *H. fraasi* to *Egertonodus* must be considered tentative in the absence of data concerning the subcranial aortic arrangement, cephalic spines, and oropharyngeal denticles.

2. HYBODONTID SYSTEMATICS

Family Hybodontidae Owen

Hybodus Agassiz, 1837

Syn. *Leiacanthus* Ag., 1837

?*Meristodon* Ag., 1843

Sphenonchus Ag., 1843 (in part)

?*Selachidea* Quenstedt, 1852

Orthybodus Jaekel, 1898

Parahybodus Jaekel, 1898

Type species: *Hybodus reticulatus* Ag., 1837

Egertonodus, g. nov.

Type species: *Hybodus basanus* Egerton, 1845

Acrodus Agassiz, 1838

Syn. *Sphenonchus* Ag., 1843 (in part)

Thectodus von Meyer and Pleininger, 1844

?*Hylaeobatis* Woodward, 1916

Type species: *Acrodus nobilis* Ag., 1838

Palaeobates Meyer, 1849

Syn. *Strophodus* Ag., 1838 (in part)

Type species: *Palaeobates angustissimus* (Ag.), 1838

Lissodus Brough, 1935

Syn. *Lonchidion* Estes, 1964

Type species: *Hybodus africanus* Broom, 1909

Polyacrodus Jaekel, 1889

Type species: *Hybodus polycyphus* Ag., 1838

Asteracanthus Agassiz, 1837

Syn. *Strophodus* Ag., 1838 (in part)

Sphenonchus Ag., 1843 (in part)

Curtodus Savage, 1867

Type species: *Asteracanthus ornatissimus* Ag., 1837

Bdellodus Quenstedt, 1882

Type species: *Bdellodus bollensis* Quenstedt, 1882

The earliest named species of *Acrodus* is *A. gaillardoti*, quoted from an unpublished Agassiz manuscript by Gaillardot (1835, p. 49). This is regarded as the type species (by monotypy) by some authors (e.g., Glikman, 1967; Johnson, 1981). Since the species is not described or defined, however, the name is unavailable and it does not constitute an indication for the genus (International Code of Zoological Nomenclature, 1985, art. 12). Agassiz (1838) described the genus and various species (including *A. gaillardoti*), but failed to designate a type species. Woodward (1916, p. 14) proposed that *A. nobilis* Agassiz be considered the type species; that decision is supported here.

Rather fewer taxa are retained within the Hybodontidae here than in the majority of previous works. In Woodward (1889a), for

example, the equivalent higher taxon (Cestraciontidae) included *Orodus*, *Campodus*, *Diclitodus*, *Sphenacanthus*, *Tristychius*, *Wodnika*, *Palaeobates*, *Hybodus*, *Acrodus*, *Asteracanthus*, *Strophodus*, *Bdelodus*, *Palaeospinax*, *Synechodus*, and *Cestracion* (= *Heterodontus*), an assemblage that admirably illustrates the Victorian propensity for erecting nongroups. Owen (1860) had earlier classified selachian fishes into four great families of equal rank: Raiidae (skates and rays), Squalidae (Recent sharks except *Heterodontus*), Cestraciontidae (*Heterodontus*), and Hybodontes (many extinct taxa).

This scheme was modified by Owen (1866) by combining the Cestracionts and Hybodonts into the suborder Cestraptorhi (fossil and Recent sharks characterized by dorsal fin spines). Since that time, the notion that *Heterodontus* is some kind of "Living Fossil" hybodontid has remained popular (e.g., Goodrich, 1909, 1930; White, 1937; Smith, 1942; Radinsky, 1961; Young, 1962; Patterson, 1966; Andrews et al., 1967; Schaeffer, 1967; Blot, 1969), despite an increasingly overwhelming body of opposing data (Brown, 1900; Zittel, 1911; Brough, 1935; Holmgren, 1941; Compagno, 1973; Reif, 1973, 1978a, 1978b; Maisey, 1975, 1977, 1978, 1982, 1983, 1984a, 1984b, 1985).

It is by now well established that the Hybodontidae are an extinct group of sharks whose cranial morphology and dermal skeleton was highly specialized. The group is probably ancient, and some Paleozoic taxa may be related to it (e.g., *Tristychius*, *Onychoselache*; Dick, 1978; Dick and Maisey, 1980). However, many other taxa have erroneously been assigned or allied to the Hybodontidae by means of homoplasies, spurious and ambiguous characters (see Maisey, 1982, p. 42 for a review), and even by no characters at all [e.g., *Orodontidae* (Woodward, 1889a, p. 229)].

3. TOOTH HISTOLOGY, TOOTH ARCHITECTURE, AND HYBODONTID PHYLOGENY

For the term "Hybodontidae" to possess any kind of taxonomic credibility, it would seem reasonable that only those taxa sharing some apomorphic peculiarities with *Hybodus*

should be admitted. In the above list, all but two of the included taxa (*Polyacrodus*, *Bdelodus*) are now known from more than isolated teeth. In most cases, parts of the endoskeleton are available, as well as dermal elements, and in future papers some of this material will be discussed (meanwhile, see Rieppel, 1981; Maisey, 1982, 1983, 1985, 1986). Nevertheless, it is the teeth which have customarily attracted the attention of paleontologists, and hybodontid tooth morphology has been central to various hypotheses of elasmobranch evolution for well over a century (e.g., Owen, 1940–45; White, 1937; Casier, 1947a–c; Radinsky, 1961; Glikman, 1964, 1967). In almost every case, however, the "*Cestracion* Ikon" of Agassiz (1833–44) and Owen (1860, 1866) has had a decided influence.

TOOTH HISTOLOGY: Hybodontid tooth histology and ultrastructure has been critically examined by Stensiö (1921), Seilacher (1943), Radinsky (1961), Patterson (1966), Reif (1973, 1978a), Johnson (1981), and Rieppel (1981), although the number of species surveyed remains a small fraction of the total described. In such circumstances there is always a danger that the paucity of data may create artificial and misleading distinctions in the mind of the investigator. A classic example of this is Glikman's (1964, 1967) major division of sharks into two infraclasses, Orthodonta and Osteodonta, and its subsequent rejection by Patterson (1966) and Compagno (1973). At face value, Glikman's suggestions amount to no more than a gross oversimplification of reality, but with the incorporation of supplementary data concerning enameloid ultrastructure (Reif, 1973, 1978a), Glikman's concept has taken on renewed significance (Maisey, 1982). Patterson's (1966) objection to Glikman's subdivision of orthodont and osteodont Hybodontidae is somewhat blunted, since it is no longer "necessary to believe that *Lissodus* and *Lonchidion* are only related to the well known Jurassic and Cretaceous species of *Hybodus* insofar as the Orthodonta and Osteodonta shared a hypothetical common ancestry in the Lower Devonian" (ibid., p. 332), although Duffin (1985) espoused the view that the *Lissodus/Lonchidion* lineage has indeed been distinct since at least the Lower Car-

boniferous. Reif's (op. cit.) discoveries fairly conclusively demonstrate what Radinsky (1961) and Patterson (1966) could only surmise, namely that tooth dentine histology has undergone parallel transformations in the Hybodontidae and Recent elasmobranchs. Under these circumstances it seems worthwhile to review available data for hybodontid teeth and, if possible, to formulate a phylogenetic hypothesis that is open to falsification or modification by the discovery of new anatomical data.

The terminology for various dentinous tissues is a complex issue that will not be appraised here (see Ørvig, 1951, 1967; Radinsky, 1961; Glikman, 1967; Rieppel, 1981; Zangerl, 1981). The observed histological variation among hybodontid teeth can be summarized as follows (mostly after Peyer, 1946, 1968; Radinsky, 1961; Patterson, 1966; Rieppel, 1981).

Teeth of *Hybodus* and *Acrodus* typically consist of a thin outer enameloid layer plus an underlying layer of pallial dentine (sensu Rieppel, 1981; = "Manteldentin" of Weidenreich, 1926), below which is a central core of osteodentine with relatively little osteonal tissue.

Teeth of *Asteracanthus* have a thin outer layer of pallial dentine, although this is sometimes lost, probably by in vivo abrasion. Below this is a layer of vascularized osteonal dentine in which the vascular canals are arranged in vertical columns, with thick areas of interosteonal tissue, all overlying a thick layer of circumpulpar dentine (Rieppel, 1981, fig. 13B, C). The lateral, noncuspid "molariform" teeth of *Heterodontus* are somewhat similar, but there only the upper region of the osteodentine has a columnar arrangement, whereas the deeper-lying part is irregularly arranged (Radinsky, 1961, p. 75). *Lisodius africanus* teeth are generally not suitable for histological study (Brough, 1935; Duffin, 1985). In "*Lonchidion*," *Palaeobates*, and *Polyacrodus* the teeth generally consist of outer enameloid and pallial dentine, overlying a thick orthodentine layer which is usually distinguished from pallial dentine by the number and size of dentinal tubules (Jaekel, 1889; Stensiö, 1921; Estes, 1964; Patterson, 1966; Rieppel, 1981; Duffin, 1985). Variation is seen in both the thickness and degree of vascular-

ization of the orthodentine, largely attributed by Stensiö (1921, p. 38) to ontogenetic differences, although Johnson (1981) suggested that some variation is related to dentitional position. In a *Polyacrodus minimus* tooth sectioned by Patterson (1966, pl. 5, fig. 1) there are traces of canals (apparently not "contained" by denteonal trabeculae) passing into the orthodentine (perhaps corresponding to "tubular" orthodentine; see Zangerl in Peyer, 1946). According to Johnson's (1981) criteria, this arrangement would be typical of an anterior tooth in *Polyacrodus*. Such vascular canals are absent from the lateral teeth of *Palaeobates angustissimus* (Patterson, 1966, pl. 5, fig. 2; Rieppel, 1981, fig. 14B) and "*Lonchidion*" spp. (Estes, 1964, fig. 2d; Patterson, 1966, pl. 5, fig. 3), and also from supposed lateral teeth of *Polyacrodus* (e.g., *P. wichitaensis*; Johnson, 1981, p. 14).

At the present time, a limited number of competing scenarios are feasible:

1. Tooth histology has changed many times, perhaps for functional reasons, and is therefore an unreliable taxonomic and phylogenetic tool (e.g., Radinsky, 1961; Patterson, 1966; Compagno, 1973).

2. Tooth histology has changed relatively few times, and is phylogenetically informative; in which case the primitive pattern for Hybodontidae could be: (a) osteodont (e.g., *Hybodus*, *Acrodus*), (b) orthodont (e.g., *Polyacrodus*, "*Lonchidion*," *Palaeobates*), or (c) columnar (e.g., *Asteracanthus*). The example cited by Compagno (1973) of histological variation between two closely related carcharhinoid taxa (*Hemipristis* and *Dirrhizodon*) seems to be exceptional, and the example given by Patterson (1966) in pristids is hardly admissible, since it concerns specialized rostral "teeth" (modified dermal denticles) rather than dentitional teeth.

The paleontological evidence for the histological instability of shark teeth is also weak, stemming mainly from studies of isolated teeth from incertae sedis taxa (e.g., *Ptychodus*, *Hylaeobatis*, "*Orodus*"). Where something is known of the anatomy other than teeth, we find that dental histology is remarkably uniform in spite of great variation in tooth morphology (and presumed function) among closely related taxa (e.g., *Hybodus*, *Acrodus*; Radinsky, 1961). On the

whole, neontological and paleontological data both support the contention that shark tooth histology is conservative, and that observed variations are potentially informative phylogenetically.

Having reached this conclusion, it is still a quantum leap to the assumption that various dental histologies each arose only once in hybodontid evolution. Nevertheless, this is the simplest falsifiable hypothesis, and as such it provides an immediate basis for further phylogenetic studies. However, there remains the controversial problem of which condition is primitive. According to Rieppel (1981, p. 351) "osteodentine has been replaced by orthodentine" (i.e., phylogenetically) in orthodont hybodontids. It is clear from Jaekel's (1889, p. 329) remarks that he, too, regarded osteodentine as phylogenetically primitive. The columnar osteodentine of *Asteracanthus* has similarly been regarded as a specialized "derivative" of osteodentine, from ancestral sharks possessing osteodont teeth (Peyer, 1946, 1968; Radinsky, 1961). Thus the view that osteodentine is primitively present in hybodontid teeth has proven attractive to many investigators, thereby strengthening the popular idea that *Hybodus* and *Acrodon* are form genera having no taxonomic reality.

This long-cherished view is somewhat undermined by ontogenetic data. According to Peyer (1968, p. 61):

in elasmobranchs a very regular coat of orthodentine is always formed first, surrounding a wide, uniform pulp cavity, even when the mode of formation of dentine changes in the further development of the tooth In *Raja*, *Mustelus*, and other elasmobranchs whose teeth consist of orthodentine, the genesis of dentine progresses during the entire period of its formation in a rather uniform way Where trabecular dentine occurs, there is a sudden, non-transitional change in the mode of formation . . . brought about by the odontoblasts which, instead of retreating in closed formation toward the center of the pulp cavity, suddenly show a seemingly irregular alignment throughout the pulp cavity.

It is clear from this developmental viewpoint that Peyer (1968) regarded the osteodont condition to be derived, since it involves secondary reorganization of odontoblast migration patterns; he placed a similar interpre-

tation on the columnar osteodentine of *Heterodontus* lateral teeth, in which the earliest-formed dentine is "compact orthodentine" (Marquard, 1946; ? = pallial dentine of Rieppel, 1981). While it might be argued that a reorganization from orthodentine to osteodentine is no more than the ontogenetic equivalent of switching from pallial dentine to orthodentine, the consequences of this switch, as far as odontoblast reorganization is concerned, are surely more profound where osteonal tissue is subsequently formed. Besides the odontoblast reorientation itself, the involvement of fibroblastic mesodermal cells (in forming the collagenous denteonal framework) is also greatly enhanced. Thus the formation of osteodentine involves considerably greater secondary modification to skeletal genome expression than does orthodentine deposition. In consequence, I concur with Peyer's (1968) opinion that osteodentine formation in elasmobranch teeth is secondary, and conclude that hybodontids (and other elasmobranchs) with orthodont teeth are probably primitive in this respect (see also Maissey, 1982, p. 28).

Outgroup comparison among Recent elasmobranchs (particularly among those taxa that are considered cladistically primitive) is relatively uninformative. *Chlamydoselachus* is orthodont (Pfeil, 1983, p. 19), but hexanchoid teeth and *Heterodontus* lateral teeth are osteodont (Agassiz, 1844; Marquard, 1946; Radinsky, 1961; Peyer, 1968). According to Compagno (1973), *Heterodontus* anterior teeth are orthodont. Among fossils, "*Cladodus*" and xenacanthid teeth sectioned by Agassiz (1844, pls. M₁, M₂) are orthodont, and most Paleozoic chondrichthyans seem to possess either orthodont or tubular "bradyodont" tooth histology, rather than irregular osteodentine as in *Hybodus*, *Egertonodus*, and *Acrodon*. Thus the stratigraphic record, incomplete though it is phylogenetically, at least hints that the hybodontid osteodont condition is derived (i.e., that *Hybodus*, *Egertonodus*, and *Acrodon* together represent a monophyletic group, albeit of form species). Further outgroup comparison with osteichthyans corroborates Peyer's (1968) contention that the osteodont condition is derived. The teeth of various Recent and fossil Actin-

opterygii and Sarcopterygii largely consist of orthodentine (Peyer, op. cit., pp. 90–118). “Labyrinthodont” folding of the dentine and enamel (e.g., *Rhizodus*, *Holoptychius*) can be so complex as to produce the appearance of osteodentine in transverse section (Peyer, op. cit., fig. 61). Among cladistically primitive Actinopterygii (e.g., *Polypterus*, *Lepisosteus*, *Amia*) the teeth also consist mainly of orthodentine (sometimes modified, e.g., into the folded “plicidentine” of *Lepisosteus*).

Provisionally accepting that osteodont Hybodontidae form a monophyletic group, it is much less clear whether to regard columnar osteodentine (e.g., of *Asteracanthus*) as an independently acquired character (i.e., from an orthodont ancestor), or as a specialization of the osteodont condition. Which viewpoint is adopted will clearly have a radical effect on one’s view of the systematic position of *Asteracanthus*. Again, perhaps the most convincing evidence comes from the ontogeny of *Heterodontus* lateral teeth, in which the first-formed osteodentine (immediately below the outer layer of pallial dentine) is arranged in columnar fashion, while subsequent osteodentine is deposited more randomly (Marquard, 1946). Corresponding modifications to dentine formation have been inferred in *Acrodus* (Radinsky, 1961). In an *Asteracanthus* cf. *reticulatus* tooth sectioned by Rieppel (1981, fig. 14B, C), the outermost denteons also form a columnar pattern, but an irregular arrangement occurs deeper within the tooth. It is tempting to suggest that the irregular osteodentine pattern (formed relatively late in ontogeny, after pallial or columnar dentine is deposited) is an extreme specialization of certain Hybodontidae (particularly those with high-crowned teeth). One consequence of this hypothesis is that the multicuspoid, high-crowned teeth observed in *Hybodus* and *Egertonodus* represent a cladistically derived pattern that has been acquired independently from other Recent and fossil taxa (e.g., “*Cladodus*,” *Xenacanthus*, *Ctenacanthus*, *Cobelodus*, *Palaeospinax*, *Synechodus*, various galeomorphs, *Chlamydoselachus*), and that the Hybodontidae are plesiomorphically characterized by tumid, low-crowned teeth (a supposition which is loosely corroborated by the stratigraphic record and by the dentition in some unde-

scribed Pennsylvanian Hybodontiformes from Kansas; Maisey, in prep.).

TOOTH ARCHITECTURE. Historically, there is uncertainty and confusion surrounding “hybodont” tooth architecture and external morphology. While many “hybodont” taxa have been described solely on the basis of teeth, the latter are difficult to define collectively in terms of unique attributes, since certain features are common to teeth of many extinct and apparently unrelated nonhybodontids such as Xenacanthidae and “clado-donts” (e.g., *Ctenacanthus*, *Cobelodus*), or to neoselachians such as *Heterodontus* and the extinct taxa *Palaeospinax* and *Synechodus* (Maisey, 1982).

In attempting to “define” a tooth from a hybodontid shark, in many respects it is easier (though systematically questionable) to compare what they lack when compared with other elasmobranch teeth. For example, the following dentitional features are generally *not* found in the teeth of taxa listed above:

1. Expanded semicircular lingual torus with median or paired articular surfaces (present in “cladodonts,” Xenacanthidae; expanded torus but no articular surfaces in *Palaeospinax*, *Synechodus*, *Orthacodus*, *Chlamydoselachus*).

2. Enameled surface of adjacent cusps is disjunct (enameled cusps separated by unenameled areas in Xenacanthidae, many “cladodonts,” some *Synechodus* spp., *Chlamydoselachus*, and some lamniforms).

3. Nonlinear progressive size reduction from the median cusp to the lateral cusps (“*Cladodus*,” *Phoebodus*, or Xenacanthidae, *Chlamydoselachus*; progressive linear reduction of cusp height only apparent in multicuspoid hybodontid teeth; a similar progressive arrangement also occurs in some fossil neoselachians, e.g., *Palaeospinax*, *Synechodus*).

4. Bradyodont crown architecture, with denteonal pores at tooth surface (n.b. heavily abraded *Asteracanthus* teeth show “pseudo-bradyodont” pattern where columnar dentine has become secondarily exposed).

5. Fusion of successional teeth (occurs in “*Pleuroodus*” teeth of *Helodus*, iniopterygians, and edestid symphyseal teeth).

6. Divided, downturned roots (lateral projections from basal plate in various neose-

lachsians, particularly Lamniformes; labiolingual projections in Xenacanthidae).

7. Specialized root foramina ("foramen individualisé" of Casier, 1947a, p. 9; see discussion below).

In some cases, hybodontid teeth are characterized only by absence of certain features (e.g., of 1, 4, 6, 7). Furthermore, in most cases these features have a more widespread (even if disjunct) distribution among Recent and fossil chondrichthyans, suggesting homoplasy. The one possible exception to this is the last character which, despite being an absence, is sufficiently unusual to have captured the attention of several investigators.

Casier (1947a, p. 9) was first to diagnose hybodontid tooth morphology by this means. His "type hybodontoid" was distinguished by (among other criteria): "L'absence de foramen individualisé (il n'y a qu'une rangée horizontale de pores, en nombre indéfini, à chacune des faces externe et interne) et le caractère très poreux de la face basilaire, correspondant à celui, très amorphe, de la structure interne, sans canaux définis, mais à grand nombre de sinus communiquant plus ou moins entre eux, pour constituer une cavité centrale, et, selon toute apparence, à une irrigation dentaire par un système vasculaire diffus."

In a review of British Wealden shark teeth, Patterson (1966) noted that several taxa possessed Casier's (1947a) "hybodontid root." Some teeth had a horizontal series of pores just below the root/crown junction (e.g., *Hybodus parvidens*; Patterson, 1966, fig. 7; *H. brevicostatus*; *ibid.*, fig. 13). In subsequent works, these pores have come to be regarded as specialized foramina (e.g., Johnson, 1981, p. 4, fig. 1; Duffin, 1985, p. 108, fig. 1). However, it is quite clear from Casier's (1947a) original description, and from his subsequent comments in that work (see also Casier, 1947b, and particularly his 1947c, p. 9 definition of the "anaulacorhize" stage: "Pas de foramens définis; en principe rien que des pores") that "pores" and "foramen individualisé" are subtly different. Thus the "specialized foramina" identified by Johnson (1981) and Duffin (1985) do not correspond to the "foramen individualisé" of Casier (1947a-c), but to the "rangée horizontale de pores . . . à chacune des faces interne et externe" of his "hybodontoid" or anaulacorhize teeth. In general, the enlarged foramina

(e.g., of hemiaulacorhize, holaulacorhize, and perhaps polyaulacorhize neoselachian teeth, *sensu* Casier, 1947c, p. 9) are located some distance below the root-crown junction. This suggests that the enlarged foramina are morphologically and perhaps functionally distinct from the row of horizontal pores.

Support for this view comes from a few acid-prepared teeth of *Hybodus reticulatus* (e.g., MCZ 780; fig. 18). On the lingual surface there is a horizontal series of pores, below which are a few larger canals (fig. 18A, C), penetrating straight through the root to emerge in the middle of the basal face (fig. 18B, D). In one example there is a median canal and a pair of lateral canals (each situated level with the penultimate lateral cusp; fig. 18A, B). The canals have a thin floor of dentine, although in another tooth from the same specimen these canals are incompletely floored, as in developing neoselachian teeth. Topographically these larger canals and their foramina are similar to the enlarged median and paired foramina of certain fossil neoselachians (e.g., *Palaeospinax*, *Synechodus*) and to corresponding enlarged canals in the roots of "*Cladodus*," xenacanthid, and *Helodus* teeth.

Hybodus reticulatus is thus an embarrassment to Casier's (1947a) "hybodontoid" tooth pattern, since the type species of *Hybodus* displays a character that "hybodonts" are supposed to lack. However we may still be justified in regarding Casier's (1947c) anaulacorhize "stage" as a valid special condition of the Hybodontidae, by emphasizing the presence of the horizontal pore system below the crown/root junction (which is apparently unique), and by deemphasizing the lack of specialized foramina ("foramen individualisé"), which are primitively present in *Hybodus reticulatus*.

Restated in this way, the anaulacorhize root architecture of the Hybodontidae is a further potential synapomorphy of the group, instead of a primitive archetype from which various neoselachian patterns might be derived. Such patterns are more readily "explained" as phylogenetic "derivatives" of the vascularization pattern and root morphology found in *Synechodus*, *Palaeospinax*, and "*Cladodus*" teeth. These extinct taxa plesiomorphically retain specialized root canals but lack the horizontal pore system of the Hybodontidae, and do not therefore possess an-

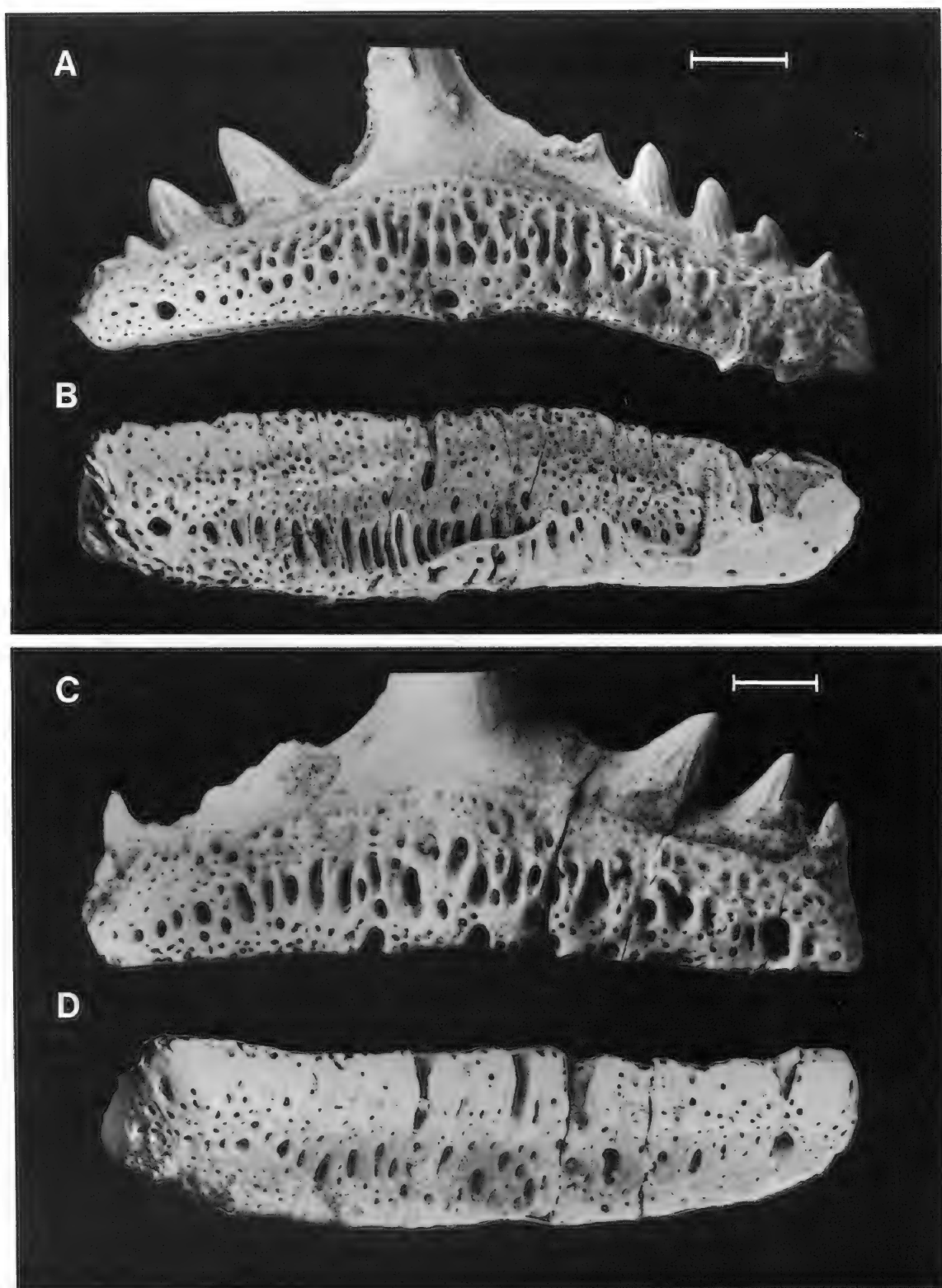


Fig. 18. SEM photographs of two *Hybodus reticulatus* teeth from MCZ 780, showing configuration of root foramina within lingual (A, C) and basal/labial (B, D) surfaces. Tooth in A and B has median and paired enlarged canals; tooth in C and D has less ordered arrangement. Immediately below the root/crown junction is a horizontal series of numerous small pores which are separated from the enlarged canals by many large and primitively irregular openings, giving the root a spongy appearance. Teeth gold-coated and examined on Cambridge Stereoscan-250 at 3 kV. Scale bars = 2 mm.

aulacorhize teeth (as defined by Casier, 1947c, and modified above).

From the above remarks it seems that tooth histology by itself does not permit the erection of any particularly convincing phylogeny of the Hybodontidae. When histological and morphological data are combined, however, some kind of transformational pattern seems vaguely recognizable, with a primitive condition of molariform anaulacorhize teeth consisting of pallial dentine overlying non-vascular orthodentine (e.g., "*Lonchidion*," *Polyacrodus*, *Palaeobates*), the acquisition of irregular osteodentine below columnar dentine (e.g., *Asteracanthus*), followed perhaps by secondary loss of columnar dentine (e.g., "*Acrodus*," *Hybodus*; fig. 19A). A slightly more parsimonious hypothesis can be formulated by assuming that the columnar osteodentine of *Acrodus* and *Asteracanthus* is a synapomorphy, since this does not involve a character reversal for the *Hybodus*/*Egertonodus* group (fig. 19B). *Hybodus* and *Egertonodus* emerge from either scenario as derived Hybodontidae united by high-crowned, multicuspid teeth; in the second scenario *Acrodus* and *Asteracanthus* also form a monophyletic group, characterized by columnar dentine within the tumid, low-crowned teeth. It remains to be seen whether these hypotheses of relationships are refuted by additional (nondentitional) data.

CONCLUSIONS

At this time it would be premature to claim anything but modest progress in unraveling the systematic relationships of the Hybodontidae. The genus *Hybodus* remains poorly diagnosed, but this is no longer simply a consequence of a lack of data. Something is now known concerning the cranial anatomy in the type species, *H. reticulatus*. Comparison with other material suggests, however, that virtually every known aspect of cranial anatomy in *H. reticulatus* also characterizes a broader group or groups (e.g., Hybodontidae, Hybodontiformes). Moreover, the status of most *Hybodus* species, founded upon isolated teeth or fin spines, remains unresolved.

Nevertheless, in a few respects the cranial anatomy of *H. reticulatus* seems to differ from that of some other taxa (notably *H. basanus* and *H. fraasi*). Optimistically, this may pre-

sage the fulfillment of a century-old prophecy, namely "that future research in regard to structures other than teeth will lead to the subdivision of the multitudinous forms hitherto grouped under one generic name" (i.e., *Hybodus*; Woodward, 1886, p. 223). It is suggested that *H. basanus* and *H. fraasi* are sufficiently distinct from *H. reticulatus* to merit their placement within a new genus (*Egertonodus*). As additional species become better known, it should be possible to elaborate the phylogeny and taxonomy of the Hybodontidae beyond the level attained here (hopefully before another century has passed!), although the vast majority of nominal species will undoubtedly remain incertae sedis taxa.

I have suggested elsewhere (Maisey, 1986) that the Hybodontidae represent an extinct group of ecological generalists with an arrested evolutionary pattern. However there is evidence of some (presumably adaptation-al) changes in tooth histology among certain hybodontid taxa. Furthermore, in at least one genus (*Asteracanthus*) it is certain that such histological modifications were accompanied by changes in palatoquadrate morphology which would presumably involve some departure from the suspensorial arrangement seen in *H. basanus* and *H. reticulatus* (Maisey, 1982). Unlike some other investigators (e.g., Radinsky, 1961; Patterson, 1966), I regard histological variation in hybodontid teeth as a potentially useful preliminary basis for phylogenetic analysis of this otherwise conservative group. The following conclusions have been drawn from the current investigation:

1. The primitive hybodontid tooth histology is orthodont (i.e., with a thin layer of enameloid and pallial dentine overlying a thicker layer of circumpulpar orthodentine), as in *Polyacrodus*, "*Lonchidion*," and *Palaeobates*.

2. At least some orthodont hybodontids possessed *Hybodus*-like cranial anatomy and triradiate cephalic spines (e.g., *Palaeobates*; Rieppel, 1981; Maisey, in prep.). Where known, the detailed cranial and cephalic spine morphology of Paleozoic Hybodontiformes, here excluded from the Hybodontidae (Maisey, in prep.), is different from that of *Hybodus*.

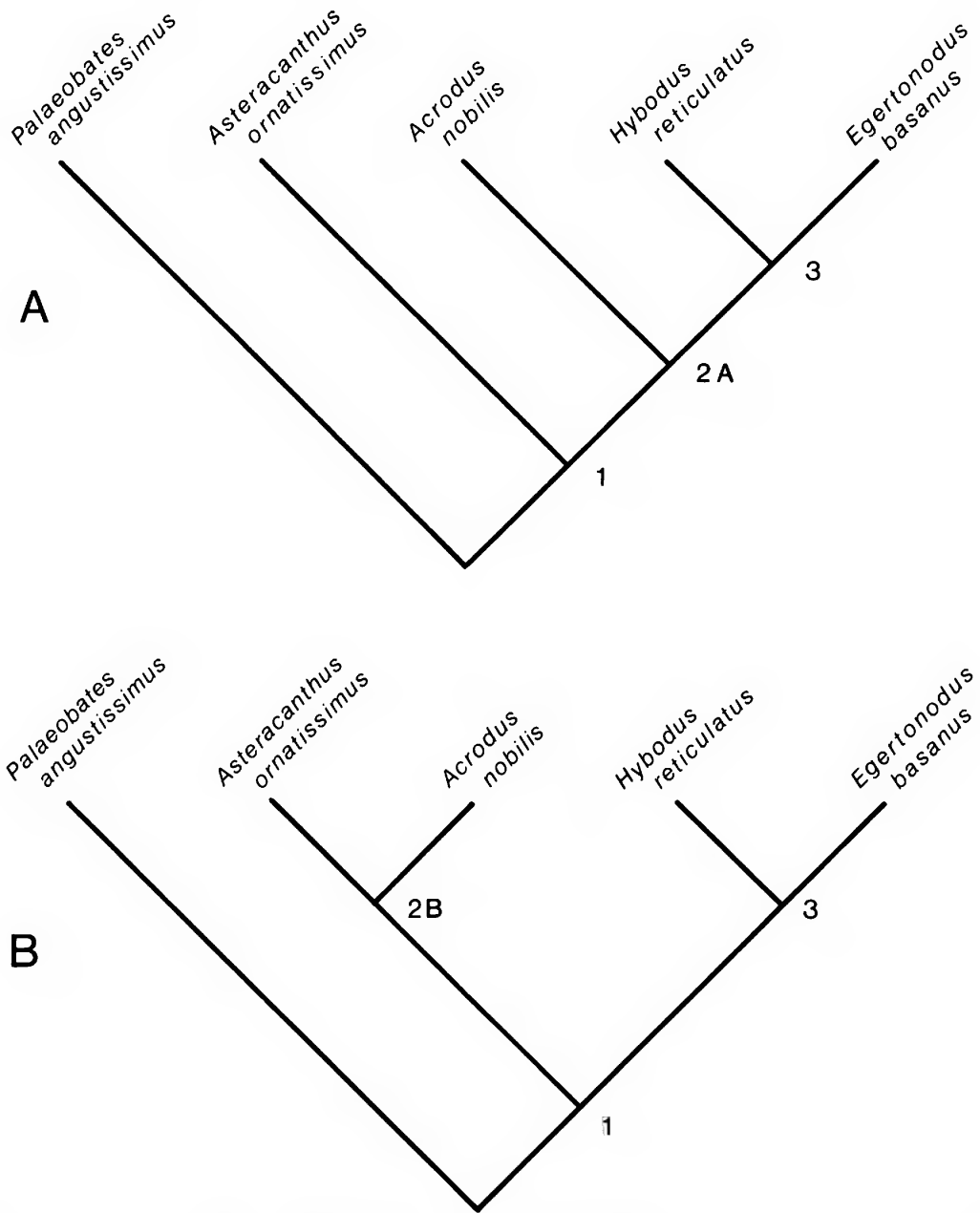


Fig. 19. Two plausible hypotheses of hybodontid relationships based on tooth histology. (A) is supported by Recent ontogenetic data for elasmobranch teeth, but involves a reversal (columnar osteodentine, acquired at node 1 and lost at node 3); (B) is more parsimonious but requires an assumption about columnar osteodentine being apomorphic. Characterization of nodes is as follows: 1, osteodentine present (primitively columnar in A, but primitively irregular in B); 2A, irregular osteodentine present; 2B, columnar osteodentine present; 3, high-crowned multicuspid teeth. In each case, molariform orthodont teeth are considered primitive, multicuspid osteodont teeth derived.

3. Ontogenetic data indicate that orthodontine, irregular osteodentine, and columnar osteodentine are deposited after the for-

mation of enameloid and pallial dentine. The formation of osteodentine involves considerably greater reorganization of scleroblasts

and fibroblasts than orthodontine deposition, however, and is consequently viewed as a derived condition of skeletal genome expression. Columnar osteodentine (if present) characteristically forms prior to irregular osteodentine, suggesting that the latter is a more extreme modification of skeletal genome expression than columnar osteodentine.

4. Some low-crowned, tumid hybodontid teeth may be orthodont (e.g., *Palaeobates*); others consist largely of columnar osteodentine (e.g., *Asteracanthus*), or of irregular osteodentine with only a thin columnar layer (e.g., *Acrodus*). Osteodont hybodontid teeth may be low- or high-crowned and multicuspid. Such high-crowned teeth are typically osteodont, suggesting that this tooth pattern is derived among Hybodontidae.

5. At least two taxa of high-crowned Hybodontidae are recognizable (*Hybodus*, *Egertonodus*).

6. Although irregular osteodentine may represent a more derived condition than columnar osteodentine (see 3 above), it is cladistically more parsimonious to regard the presence of columnar osteodentine as a synapomorphy of *Acrodus* and *Asteracanthus*.

7. This phylogeny predicts that Hybodontidae ancestral to the *Hybodus*/*Egertonodus* and *Acrodus*/*Asteracanthus* groups would have possessed low-crowned osteodont teeth, lacking the columnar variety of osteodentine. Such a tooth histology does not seem to have been described, although irregular nondenteonal canals are present in some orthodont teeth (e.g., Patterson, 1966, pl. 5, fig. 1).

8. The "anaulacorrhize" architecture of hybodontid teeth is probably apomorphic, rather than a primitive pattern as suggested by Casier (1947a-c).

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